Genomic data reveal a protracted window of introgression during the diversification of a neotropical woodcreeper radiation

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GENOMIC DATA REVEAL A PROTRACTED WINDOW OF INTROGRESSION DURING THE DIVERSIFICATION OF A NEOTROPICAL WOODCREEPER RADIATION

ABSTRACT

The incidence of introgression during the diversification process and the timespan following divergence when introgression is possible are poorly understood in the Neotropics where high species richness could provide extensive opportunities for genetic exchange. We used thousands of genome-wide SNPs to infer phylogenetic relationships, calculate ages of splitting, and to estimate the timing of introgression in a widespread avian Neotropical genus of woodcreepers. Five distinct introgression events were reconstructed involving taxa classified both as subspecies and species including lineages descending from the basal–most split, dated to 7.3 million years ago. Introgression occurred between just a few hundred thousand to about 2.5 million years following divergence, suggesting substantial portions of the genome are capable of introgressing across taxa boundaries during a protracted time window of a few million years following divergence when reproductive isolation is incomplete and introgression is possible. Despite this protracted time window, we found that the proportion of the genome introgressing (6 to 11%) declines with the time of introgression following divergence, suggesting that the genome becomes progressively more immune to introgression as reproductive isolation increases.

Keywords: introgression, hybridization, speciation, *Dendrocincla,* Neotropics.

INTRODUCTION

Genomic datasets have now made it clear that hybridization is a process that often occurs during the diversification process (Taylor and Larson 2019). Following population divergence from a common ancestor, diverging lineages possess a time window during which incomplete reproductive barriers may allow for hybridization and introgression to influence the diversification process. Shortly after population differentiation, introgression may be highly prevalent given insufficient time to accumulate reproductive barriers, leading to population fusion upon secondary contact (Rhymer and Simberloff 1996; Taylor et al. 2006; Kearns et al. 2018). Such population fusion has the effect of hindering diversification and is likely to play a key role in accelerating extinction rates in regions where taxa come into geographic contact after short durations in allopatry (e.g. high latitudes: Weir and Price 2011a; Cutter and Gray 2016). In contrast, during late stages of speciation, hybridizing taxa may be unlikely to experience introgression because sufficient numbers of genetic incompatibilities render the genome largely immune to introgression (so called "genomic speciation": Gompert et al. 2017; Nosil et al. 2017; Pulido-Santacruz et al. 2018). However, at intermediate levels of divergence, genetic incompatibilities may render hybrids less fit, thereby preventing species differentiation upon geographic contact, but may be of insufficient number to render the majority of the genome immune to introgression. Genomes at this stage may be semipermeable to introgression, with neutral portions of the genome not closely linked to genetic incompatibilities introgressing freely, while adaptive introgression may occur at genes in which alleles convey an adaptive advantage in a heterospecific genomic background (Barton 1979; Harrison 1993; Harrison and Larson 2014; Payseur and Rieseberg 2016). Introgression at this intermediate stage could positively influence

47 diversification. For example, adaptive introgression of alleles conveying resistance to diseases
48 (Deng et al. 2016) or ecological adaptation (Whitney et al. 2010; Jones et al. 2018) could allow a
49 species to expand its geographic range leading to increased opportunities for allopatric speciation
50 and diversification and even promote adaptive radiations (Meier et al. 2017; Marques et al. 2019).
51 Reproductive isolation could also be promoted when populations of a species each exchange
52 genetic material with different donor species, leading to the accumulation of genetic
53 incompatibilities between populations (e.g. Corcoran et al. 2016). Despite the importance of
54 introgression in either hindering or aiding diversification, we still have only a limited
55 understanding of the prevalence of introgression, the length of the time window following
56 divergence when introgression is possible and the proportion of the genome that is capable of
57 introgressing. This is especially true of tropical regions which have received relatively less study
58 compared to high latitude species.
59 High species richness in the Neotropics may provide extensive opportunities for
60 introgression during diversification and a few studies have found evidence for introgression in
61 groups that are rapidly diversifying (e.g. *Heliconius* butterflies: Mallet et al. 2007; Pardo-Diaz et
62 al. 2012; Martin et al. 2013; Merot et al. 2017, freshwater *Xiphophorus* fishes: Cui et al. 2013;
63 Schumer et al. 2013, 2016, island radiations such as *Geospiza* finches: Grant and Grant 2015; and
64 recently derived groups such as high Andean siskins; Beckman et al. 2018). Several key factors
65 may affect the prevalence of introgression in continental radiations of the Neotropics. First, traits
66 important for both pre-zygotic (e.g. song and plumage colouration in birds; Martin et al. 2010;
67 Weir and Wheatcroft 2011; Weir et al. 2012) and extrinsic post-zygotic (e.g. climatic niche in
68 birds; Lawson and Weir 2014) reproductive isolation are known to evolve more slowly than at
69 high latitudes in some groups. A comparative analysis quantifying response to song playback

between more than 89 pairs of closely related allopatric species and subspecies estimated that Amazonian taxa take about 3 million years of separation for aggressive levels to heterotypic playback to decline to half that seen in response to playback of their own taxon's song (Weir and Price 2019). In contrast, high latitude taxa require only half a million years to achieve the same level of song discrimination. Slow tropical evolution of species recognition may allow for introgression for a longer time window following divergence from a common ancestor, compared to high latitudes. Analysis of ages of avian species pairs with hybrid zones demonstrate that all latitudes contain young species pairs with hybrid zones, but hybrid zones persist in some Neotropical species that diverged from a common ancestor as long as 4 million years ago (Mya) (Weir et al. 2015; Pulido-Santacruz et al. 2018), demonstrating a protracted period when premating isolating barriers are poorly developed and hybridization is possible. Second, tropical avian species achieve secondary sympatry at a slower rate compared to high latitude species. The delay in sympatry may result from the slow rate of evolution, with taxa getting stuck for long periods of time in a parapatric state with their geographic ranges separated by narrow hybrid zones (Weir and Price 2011a). Prolonged parapatry of incompletely reproductively isolated taxa in the tropics may increase opportunities for introgression during the diversification process.

Introgression in the Neotropics could also be promoted by weak or semipermeable geographic barriers. For example, Amazonian rivers are often believed to form barriers to gene flow promoting diversification of understory forest birds and other groups (e.g. Haffer 1997; Naka and Brumfield 2018). However, recent studies have demonstrated the frequent occurrence of hybrid zones in headwater regions where rivers cease to act as dispersal barriers during interglacial periods of maximal forest expansion (Haffer 1997; Naka et al. 2012; Weir et al. 2015; Pulido-Santacruz et al. 2018), and introgression during the diversification process could be

93 common. Rivers may also experience periods of course changes which transfer local populations
94 from one river bank to the other, leading to introgression. Other Neotropical geographic barriers
95 may also be leaky. For example, temporary (and perhaps periodic) wet forest corridors have
96 previously been proposed to have connect lowland wet forests of the Amazon and Central
97 America and of the Amazon and the Atlantic forest of Brazil during wetter periods and may have
98 likewise provided brief periods for geographic contact and introgression during the
99 diversification process (Gentry 1982; Costa 2003; Batalha-Filho et al. 2013).
100 Our ability to generate large-scale genome-wide datasets opens a promising avenue for
101 investigating the genomic signatures of hybridization during the evolutionary history of
102 diversification in the Neotropics. In particular, the presence of hybridization during
103 diversification can now be better distinguished from other processes such as incomplete lineage
104 sorting. One test – ABBA / BABA – has been specifically useful in differentiating hybridization
105 between lineages from incomplete lineage sorting using genome-wide SNP datasets (Green et al.
106 2010; The Heliconius Genome Consortium 2012; Eaton and Ree 2013; Martin et al. 2014;
107 Fontaine et al. 2015). This test utilizes four species – one outgroup and three in-group species –
108 and analyzes how bi-allelic SNPs (with alternative alleles coded as A and B) evolve along the
109 phylogeny for these four species (see Fig. 2). Of the three ingroup species, species 1 and species
110 2 are most closely related (carrying different alleles A and B), species 3 carries the derived allele
111 (B). Hence, there are two possible configurations: either (((A,B)B)A)or (((B,A)B)A). If no
112 hybridization has occurred and under the hypothesis of shared ancestral polymorphism, the
113 number of loci exhibiting ABBA and BABA configurations are expected to be equal. Deviations
114 from that expectation are interpreted as evidence of introgression between species 3 and species 1
115 (if there is an excess of BABA patterns) or species 2 (if there is an excess of ABBA patterns)

(Durand et al. 2011). Related tests allow for the proportion of the genome introgressing between two species to be estimated (Martin et al. 2015)

Here, we used the ABBA-BABA and related statistics to determine the timing, prevalence and magnitude of introgression events during the diversification of a Neotropical avian genus – the *Dendrocincla* woodcreepers. This genus is distributed in humid forests throughout lowland regions of Central and South America as well as in cloud forest along the Andes (Hoyo et al. 2003). Beginning *ca*. 7 Mya (Weir and Price 2011b), *Dendrocincla* has diversified into a total of 26 subspecies which are grouped into six currently recognized species: *D. tyrannina, D. merula, D. fuliginosa, D. homochroa, D. anabatina,* and *D. turdina* (Remsen Jr. et al. 2018). Phylogeographic analysis has demonstrated that a number of subspecies are deeply diverged genetically (Weir and Price 2011b; Schultz et al. 2019), and some of these could represent distinct species. Available phylogenetic studies of the genus are based on just a few loci and show no consensus on deeper level phylogenetic relationships as well as between some of the relationships between subspecies within species (Derryberry et al. 2011; Weir and Price 2011b; Schultz et al. 2019). These inconsistencies may be the result of insufficient data or errors in inference. Alternatively, hybridization between species and subspecies may account for conflicting topologies.

Dendrocincla is typical of many morphologically cryptic, understory forest bird groups of the Neotropics, thus is a good group to test for introgression during the diversification process because many species or subspecies are parapatric (e.g. come into geographic contact with no more than 100km of geographic overlap) or sympatric, thus increasing the odds of introgression, and at least one pair of deeply diverged subspecies currently forms a hybrid zone where their populations come into geographic contact (*Dendrocincla f. atrirostris* and *D. f. rufoolivacea*)

(Weir et al. 2015). This hybrid zone is remarkable because the subspecies pair are estimated to have diverged from a common ancestor *ca*. 2.5 to 3 Mya, demonstrating incomplete reproductive isolation despite their old age. This hybrid zone includes both early-generation hybrids and backcrossed individuals, suggesting that introgression between deeply diverged *Dendroncincla* taxa may be possible (Weir et al. 2015). However, whether strong selection against backcrossed individuals effectively prevents the movement of heterospecific alleles outside of hybrid zones such as this one, is unknown for *Dendrocincla*. If loci are capable of escaping the hybrid zone region and introgressing into the allopatric regions of a species' geographic range, then a genomic signature of introgression may be commonly detected during diversification.

A robust species tree for the whole genus using genome-wide data is necessary to determine the frequency and magnitude of introgression and the length of the time window following divergence when introgression is possible. Here we use genome-reduction Genotyping-by-Sequencing (GBS; Elshire et al. 2011) to build a species tree and to test for a genome-wide signature of introgression using the ABBA/BABA testing framework. We predict that introgression will be absent between allopatric taxa that are geographically distant, will be most likely between allopatric taxa that are geographically proximate and between parapatric taxa whose ranges abut. In contrast, we expect minimal introgression from broadly sympatric taxa. Despite providing the greatest geographic opportunity for introgression, sympatric taxa generally have developed substantial reproductive isolation thus limiting opportunities for introgression (Weir and Price 2011a). We also predict that the proportion of the genome introgressing will be inversely related to the time since divergence from a common ancestor with introgression occurring a short time after divergence allowing both neutral and selected loci to introgress while

introgression occurring long after divergence will be restricted to a much smaller proportion of the genome due to a longer period for intrinsic post-mating isolation to develop.

METHODS

Population sampling

We obtained genetic data for 87 specimens, representing all six recognized species and 19 of 26 species and subspecies in the genus (Figure 1 and Table S1 in supporting information). Importantly, a recent phylogeographic study (Schultz et al. 2019) sequenced a single nuclear gene and mitochondrial DNA for all subspecies of *D. fuliginosa* and found that the four subspecies which we failed to sample do not represent genetically diverged lineages but rather were nested phylogenetically within subspecies we did sample (e.g. *D. f. lafresnayei* is nested within the sampled *D. f. ridgwayi*; *D. f. deltana* and *D. f. barinensis* were nested with the sampled *D. f. meruloides*; *D. f. phaeochroa* was nested with the sampled *D. f. neglecta*). We thus had complete sampling of all phylogenetically distinct subspecies within *D. fuliginosa*. Specimens and tissue samples were collected during field expeditions to Panama: from February to May 2004, Brazil: from April to July 2012 and January to March 2015, or were obtained from The Field Museum of Natural History (FMNH), Museu Paraense Emilio Goeldi (MPEG), University of Kansas Natural History Museum (UK), Louisiana State University Museum of Natural Science (LSUMZ) and Smithsonian Tropical Research Institute (STRI).

DNA isolation and SNP genotyping

183 Genomic DNA was extracted from blood or muscle tissue using the EZNA Tissue DNA
184 Kit (Omega Bio-Tek). DNA was concentrated to 30 ng/ul, quantified with picogreen and sent to
185 the Cornell Institute for Genomic Diversity for Genotyping by Sequencing (GBS; Elshire et al.
186 2011). With this method, the genomic DNA of each individual was randomly digested using the
187 PstI restriction enzyme and multiple libraries were constructed (these included both *Dendrocincla*
188 and other passerine samples), with 95 individuals uniquely barcoded in each library and each
189 library sequenced on a single lane of Illumina HiSeq 2000 platform. We obtained a total of
190 978,473 raw reads for all specimens and used the STACKS pipeline v 1.35 (Catchen et al. 2013)
191 for de-multiplexing, to prune adaptor sequence and to trim reads to 90 base pairs. Single-
192 nucleotide polymorphisms (SNPs) were called using the reference genome pipeline of STACKS
193 2.4 (Catchen et al. 2013). We used an unpublished reference genome of another woodcreeper
194 species (*Xiphorhynchus elegans*) for this pipeline. Briefly, to generate this reference, we sent
195 pectoral muscle from a single individual of *Xiphorhynchus elegans* (collector number JTW1128)
196 to Hudson Alpha who generated a single Chromium X library which was paired-end sequenced
197 (with median 306 bp insert size) along with one other avian genome on a single lane of HiSeq X.
198 We assembled the 522 million reads using default settings in Supernova 1.2.2 (Weisenfeld et al.
199 2017). The resulting genome assembly comprised 1680 scaffolds greater than 10 Kb in length, a
200 contig N50 of 108 Kb, a scaffold N50 of 2.04 Mb, an assembly size (including only scaffolds
201 greater than 10 kb) of 994.1 Mb (slightly smaller than the expected 1.1 to 1.2 Gb size typical for
202 passerine birds) and a mean depth of coverage of 43x. De-multiplexed *Dendrocincla* reads were
203 aligned to the reference using the very sensitive option of Bowtie2 v 2.3 (Langmead and Salzberg
204 2012) and SNPs were called using *ref_map.pl* routine from STACKS 2.4 (Catchen et al. 2013).

Three datasets were extracted and filtered using VCFtools v 0.1.16 (Danecek et al. 2011): A) The phylogeny dataset used to generate a maximum likelihood phylogeny and a species tree for all 87 individuals. A minimum depth of coverage of 5x was required to retain a genotype call for an individual at a given locus and loci with more than 75% of individuals with missing calls were excluded. To reduce the probability of retaining SNPs artificially generated by aligning paralogues together, we excluded SNPs that had very high coverage (exceeding the 95th percentile) and for which more than 75% of diploid samples were heterozygous. SNPs in which the minor allele had fewer than three copies (unlikely to be phylogenetically informative) were excluded and SNPs were thinned to at most 1 SNP per 10,000 bp. Heterozygous individuals for a SNP were coded with standard ambiguity codes. A total of 24,130 SNPs were retained. B) ABBA/BABA dataset. We extracted the individual representative of each taxon with highest coverage (19 individuals). As the ABBA / BABA test utilizes haploid sequences (i.e. a random allele is chosen for each heterozygous site) accurate genotype calls using high depth of coverage is not required. To increase the number of loci retained, we filtered individuals to have a minimal depth of coverage of only 3x. We applied the other filters used in the phylogeny dataset except that we allowed SNPs to be every 5,000 bp apart (to retain more SNPs). For every set of four sequences (e.g. P1, P2, P3 and Outgroup) used in an ABBA / BABA test, SNPs with missing data were excluded and individuals with sequenced copies of both alleles at a SNP were randomly assigned one of the two alleles. These final datasets of four sequences ranged in size 2,030 to 6,174 SNPs. C) G-PhoCS datasets. For the same 19 individuals used in the ABBA / BABA dataset we used the same filtering strategy except we required a higher minimum depth of coverage (8x) and required that all individuals have genotype calls in order for a SNP to be retained. We thinned SNPs to be at least 10,000 bp apart. We then extracted the 90 base pair

228 reads associated with these SNPs for a final dataset of 390 loci totalling 35,100 nucleotide
229 positions. These loci often had multiple SNPs.
230
231 **Phylogenetic analyses**
232 We generated a maximum likelihood phylogeny from our concatenated dataset of 24,130
233 SNPs using IQTree 1.6.10 (Nguyen et al. 2015). The phylogeny was used to assess whether
234 subspecies are monophyletic. Leaché et al. (2015) demonstrated that topologies estimated with
235 concatenated SNPs (invariant sites removed; as done here) are very similar to topologies
236 estimated with full sequences, hence suitable for phylogenetic inferences. We used *Deconychura*
237 as an outgroup, generally used default options but allowed the program to estimate the best model
238 of sequence evolution and used 1,000 bootstrap analyses to assess node support on the maximum
239 likelihood tree (options: -st DNA -m MFP+MERGE -bb 1000 -redo).
240 A species tree was then inferred using the coalescent-based quartet method SVDquartets
241 (Chifman and Kubatko 2014) implemented in PAUP* v4a165 (Swofford 2002). All 87
242 individuals were assigned to their respective species or subspecies and used to estimate the
243 topology. SVDquartets took the set of 24,130 bi-allelic SNPs (coded as nucleotides) and infered
244 quartet trees for all subsets of four species. SVDquartets assumes each site has its own genealogy
245 drawn from the coalescent model and has been shown to perform better as compared to other
246 methods for species inference when gene flow is present (Chifman and Kubatko 2014; Long and
247 Kubatko 2018). We sampled all possible quartets and the true quartet topology for each sampled
248 quartet was inferred using the lowest SVD score. We assembled the set of inferred quartet trees
249 into a species tree using a modified version of the Quartet FM algorithm called QFM in
250 PAUP*(Reaz et al. 2014). Uncertainty in the inferred relationships was quantified using non-

parametric bootstrapping with 1,000 replicates. *Deconychura longicauda* was used as an outgroup to root the analysis.

We fixed the species–tree topology obtained from SVDquartets (excluding the outgroup) and used the generalized phylogenetic coalescent sampler G-PhoCS v 1.3 (Gronau et al. 2011) to estimate node ages. Here node ages represent dates of population splitting. Sixteen independent 200 million step runs of G-PhoCS were obtained, each using a 10,000 step burn-in and with every 10^{th} step in the post burn-in sampled. Post burn-in samples were pooled across the 16 runs and median node ages and 95% confidence intervals were obtained for each node. We calibrated the median node age for the basal split within *Dendrocincla* with an age of 7.3 Mya obtained from a previously dated mitochondrial phylogeny for the genus (Weir and Price 2011b) which used the Passerine mitochondrial mutation rate of 2.1% (Weir and Schluter 2008). This calibration approach assumes that there has been no mitochondrial DNA introgression across the basal node in *Dendrocincla*. The higher-level topology of the mitochondrial phylogeny is identical to that uncovered here for our genome-wide nuclear dataset suggesting that if mitochondrial introgression did occur, it likely happened shortly after initial divergence and thus will have minimal impact on the calibration approach used here.

Test for Introgression

We constructed 239 ABBA/BABA tests (Table S2) using the topology from the species tree generated by SVDquartets. Outgroup taxa should be free of introgression. Given that we found evidence of introgression between lineages descending from the basal-most node in *Dendrocincla,* we restricted our use of outgroup to *Deconychura longicauda* which is closely related to *Dendrocincla* (Derryberry et al. 2011). Only loci with ABBA or BABA allelic

274 configurations for P1, P2, P3 and O are used in which A and B are alternative alleles for a bi-
275 allelic SNP.

276 Introgression may have occurred between current taxa that appear at the tips of the
277 phylogeny or may have occurred deeper in the phylogeny between ancestral lineages which have
278 since diverged into clades of multiple tip taxa. Here we used the principle of parsimony to
279 estimate the total number of introgression events and to determine where on the phylogeny
280 introgression occurred and the approximate time of introgression (see Fig. 3). For example, we
281 assumed that if all the taxa in a clade (each treated as a P3 species in multiple ABBA/BABA
282 tests) showed evidence of significant introgression with a P1 or P2 species, then a single
283 introgression event occurred involving the ancestor of the P3 clade rather than multiple
284 introgression events involving each P3 species (see example in Fig. 3B). This parsimony
285 approach also had the effect of reconstructing the timing of introgression to have occurred closer
286 to the time of divergence when reproductive isolation would be less well developed, and
287 introgression would have been more likely.

288 For the example phylogeny of five extant taxa in Fig 3, eight ABBA/BABA tests would
289 be performed and would allow us to infer whether introgression involved terminal branches or
290 internal branches of the phylogeny. The timing of introgression can then be determined by using
291 the younger of the two ancestral nodes leading to the two lineages as the oldest time when
292 introgression could have occurred while the youngest time for introgression would be the age of
293 the oldest of the daughter nodes immediately descending from these lineages or would be the
294 present if both lineages are tip taxa (see example in Fig. 3B). The ABBA/BABA approach tests
295 for introgression between most pairs of lineages, both at the tips as well as ancestral lineages
296 represented by internal branches, but cannot be used to test for introgression between sister

297 lineages including sister taxa at the tips of a phylogeny or between ancestral sister lineages (e.g.
298 the two immediate branches descending from the basal split within a phylogeny).
299 ABBA/BABA tests were conducted in R using the package *evobiR* (Blackmon and
300 Adams 2015). Standard errors and significance were assessed using 10,000 bootstrap datasets.
301 Statistical significance of *D* was calculated by converting the range of standard errors into a two-
302 tailed *p*-value, and using α=0.005 as a conservative cut-off following other authors (Eaton and
303 Ree 2013; Streicher et al. 2014), which have also found that significant *D* values can be obtained
304 from very few SNPs following the ABBA/BABA pattern. We agree with these authors in
305 reporting tests as significant only when at least 50 SNPs with ABBA or BABA patterns were
306 present.
307 For significant ABBA / BABA tests we used the f_{hom} statistic (Martin et al. 2015) to
308 estimate the proportion of the genome that experienced introgression. This statistic replaces either
309 the P1 or P2 species that had an excess of the derived allele (B) with the P3 species. Thus, rather
310 than testing P1, P2, P3 and Outgroup, we test P1, P3, P3 and Outgroup for a test in which P2
311 shared more derived alleles with P3. The statistic follows:
312 $$f_{\text{hom}} = (\text{ABBA1} - \text{BABA1}) / (\text{ABBA2} - \text{BABA2})$$ Equation 1
313 where ABBA1 and BABA1 refer to the original number of ABBA and BABA SNPs for the P1,
314 P2, P3, Outgroup test while ABBA2 and BABA2 refer to the number for the test where P1 or P2
315 (which ever has greatest number of derived alleles) is replaced with P3. This statistic provides an
316 estimate for the proportion of the genome that has introgressed and assumes that P3 introgressed
317 into P1 or P2 rather than the reverse. For further details and rational see Martin et al. 2015.

We used least squares regression to fit a linear model (R function *lm*) and non-linear least squares regression (R function *nlm*) to fit a model of exponential decay to model the change in f_{hom} as a function of lineage age when introgression occurred. The two models had the form:

$$f_{hom}(t) = f_{hom}0 - bt \quad \text{Equation 2}$$

$$f_{hom}(t) = f_{hom}0 + K(1\text{-}\exp(\text{-}Kt)) \quad \text{Equation 3}$$

where $f_{hom}(t)$ is the value of f_{hom} for lineages of age t when introgression occurred, $f_{hom}0$ is the proportion of the genome introgressing when lineage age is 0 and b is the slope of the linear and K is a parameter of the exponential decay model. The exponential decay model was chosen because it roughly approximates the expected decline in hybrid fitness when reproductive isolation is driven mostly by the accumulation of genetic incompatibilities. The two model fits were compared with Akaike Information Criterion (AIC) and the one with the lowest AIC value was chosen as best fit.

RESULTS

Phylogenetic relationships

The maximum likelihood phylogeny of concatenated SNPs produced a generally well supported topology with most taxa monophyletic (Fig 4). Most subspecies were monophyletic with strong support with three exceptions: support for monophyly of *D. m. merula* and *D. m. obidensis* was low, *D. m. castanoptera* was paraphyletic with respect to *D. m. badia* (with our sole sample of *D. m. castanoptera* from the interfluve between the Xingu and Tocantins rivers grouping with *D. m. badia*, suggesting that populations from this interfluve should either be transferred to *D. m. badia* or be recognized as a new subspecies) and the two samples of *D. f.*

340 *meruloides* were nested within those of *D. f. neglecta*, contrary to two studies which found these
341 taxa to be reciprocally monophyletic, but whose analyses were based on few genes and were
342 dominated by a mitochondrial DNA signal (Weir and Price 2011b; Schultz et al. 2019).
343 Phylogenetic analysis in SVDquartets produced a robust species tree (Fig 5). Phylogenetic
344 relationships among 18 *Dendrocincla* taxa tested were generally well-supported, with only three
345 nodes showing bootstrap values less than 95% and only one node with bootstrap support less than
346 80% (Fig. 5). Relationships among taxa were identical on the maximum likelihood and species
347 trees. Five of the six currently recognized species within *Dendrocincla* are monophyletic (*D.*
348 *tyrannina, D. merula, D. turdina, D. homochroa*, *D. anabatina*) with *D. fuliginosa* paraphyletic
349 with respect to *D. anabatina.* Previous analyses recovered a strong sister relationship between *D.*
350 *f. ridgwayi* and *D. f. meruloides* (Weir and Price 2011b). Here we found that *D. f. neglecta* and *D.*
351 *f. meruloides* are sisters and that *D. f. ridgwayi* is the next closest relative to these. Additionally,
352 *D. f. fuliginosa* and *D. f. rufoolivacea* are more closely related to one another than with *D. f.*
353 *atrirostris*, and there is strong support for the placement of *D. f. atrirostris* which was previously
354 uncertain when analyzing only a small number of genes (Weir and Price 2011b; Schultz et al.
355 2019). An earlier study recovered low support for the sister relationship between *D. merula* and
356 *D. tyrannina* (Weir and Price 2011b). Here, this relationship is strongly supported.
357 Dates of population splitting estimated on the species tree topology using G-PhoCS
358 suggest an early divergence between the *D. tyrannina* complex and the *D. merula* complex,
359 which happened shortly after the basal split within the genus (Fig. 5). Likewise, *D. homochroa*
360 and the *D. fuliginosa* / *D. anabatina* / *D. turdina* clade split from a common ancestor shortly after
361 the basal split. Our dating suggests a date of splitting between *D. turdina* and *D. fuliginosa* / *D.*
362 *anabatina* of ca. 5 Mya consistent with the recent recognition of *D. turdina* as a species distinct

363 from *D. fuliginosa* to which it was once considered conspecific. Likewise, *D. m. merula* and *D.*
364 *m. obidensis* diverged from other subspecies in the *D. merula* complex between 4 and 5 Mya
365 consistent with two distinct species, as has previously been suggested (Willis 1979). *D. m.*
366 *merula* and *D. m. obidensis* have a reddish-brown rather than a gray or blue-gray iris found in the
367 remainder of the complex, they are substantially larger, have darker overall plumage, and appear
368 to be differentiated in both song and calls (though a systemic review of vocalizations is needed).
369 The differences in behaviour, size, plumage, and genetics together with the lack of evidence from
370 ABBA / BABA tests for introgression with other members of the complex (see below) lead us to
371 recommend its treatment as a distinct biological species.
372 The sampled subspecies of the *D. fulignosa* / *D. anabatina* complex clade indicate a
373 protracted history of divergence dating back to about 3 Mya when *D. f. atrirostris* diverged from
374 the remainder of the complex. The placement of *D. anabatina* within *D. fuliginosa* renders the
375 latter paraphyletic. A sensible approach would be to recognize four clades within the complex
376 that diverged between two and three million years ago as distinct biological species: 1) *D. f.*
377 *atrirostris*, 2) *D. anabatina* (which is sympatric with *D. f. ridgwayi* and thus represents a distinct
378 biological species), 3) *D. f. fuliginosa* together with *D. f. rufoolivacea*, and 4) the clade
379 containing *D. f. ridgwayi*, *D. f. neglecta*, and *D. f. meruloides* (and also including the unsampled
380 *D. f. lafresnayei*, *D. f. barinensis*, *D. f. phaeochroa*, and *D. f. deltana* subspecies). However,
381 despite its deep phylogenetic divergence, *D. f. atrirostris* is very similar morphologically and in
382 song to the geographically adjacent *D. f. rufoolivacea* with which it forms a hybrid zone (Weir et
383 al. 2015). Nevertheless, the hybrid zone appears to be narrow and we find no evidence from the
384 ABBA / BABA test indicating that introgression has occurred between these two lineages,
385 arguing for their species status. Two other old but cryptic lineages have geographically

386 concordant hybrid zones and show clear signs of strong post-mating reproductive isolation
387 (Pulido-Santacruz et al. 2018). Further work will be needed to determine if younger members of
388 the *D. fuliginosa* complex are also specifically distinct.
389
390 **Test for introgression**
391 Fifty nine ABBA / BABA tests met our minimum cut-off of possessing at least 50 ABBA
392 or BABA sites and were tested for a significant value of *D* (Table S2). Twelve of these 59 tests
393 uncovered significant gene flow (Table 1). Using the assumption of parsimony these would
394 represent as few as five introgression events. All members of the *D. fuliginosa/anabatina* clade
395 (when treated as P3) suggested introgression with *D. merula* (P1) with respect to *D. tyraninna*
396 (P2) (Table 1). We interpret these seven tests to represent a single introgression event involving
397 the ancestral branch preceding the *D. fuliginosa* complex and the ancestral branch preceding the
398 *D. merula* complex. Likewise, both *D. turdina turdina* and *D. t. taunayi* (as P3) supported
399 significant introgression with *D. f. atrirostris* (P2) which we interpret as a single introgression
400 event between the ancestral branch preceding the *D. turdina* complex and *D. f. atrirostris*. We
401 also found evidence of an introgression event between *D. anabatina* and the ancestor of the clade
402 including *D. f. neglecta, D. f. meruloides* and *D. f. ridgwayi* (interpreted as a single event),
403 between *D. rufoolivacea* and the ancestor of *D. meruloides* and *D. neglecta* (assumed to be one
404 event), and between *D. f. ridgwayi* and *D. f. meruloides*.
405 Introgression events are dated from near the present to about 5 million years ago (Fig. 6), but no
406 events were reconstructed during the first 2 million years of the genus despite the presence of
407 ancestral branches in the phylogeny at this time of divergence which form valid ABBA/BABA
408 tests. Introgression happened from just a few hundred years to about 2.5 million years following

409 divergence from a common ancestor (Fig. 6). The proportion of introgression as measured by the
410 f_{hom} statistic ranged from 0.051 to 0.11 for the 12 significant ABBA / BABA tests. Multiple
411 ABBA / BABA tests supporting the same ancestral introgression events were averaged, resulting
412 in a range of f_{hom} from 0.057 to 0.11. When testing the relationship of f_{hom} and lineage age when
413 introgression occurred we also included *D. f. atrirostris* and *D. f. rufoolivacea* which currently
414 possess a hybrid zone, but whose ABBA/BABA test was not significant. . The relationship
415 between averaged f_{hom} and the time between divergence and introgression was substantially
416 better fit by the exponential decay model ($f_{hom}0$ = 0.12, b =0.0045) than the linear model ($f_{hom}0$
417 = 0.13, b = -0.034), with the former having an AIC value 5.9 units lower than then latter (Fig.
418 6B).

419 **DISCUSSION**

420 We used a phylogenetic approach to test for introgression among species and subspecies
421 and found that introgression in *Dendrocincla* was fairly common (at least 5 events for a
422 phylogeny with only 18 taxa), as has been found for other tropical (e.g. Martin et al. 2013) and
423 temperate clades (e.g. Sullivan et al. 2014), and that it often involved the sharing of substantial
424 amounts of the genome (ranging up to 11%). Our analyses using the ABBA / BABA test
425 uncovered clear genetic evidence for at least five distinct introgression events between non-sister
426 taxa. The actual number of introgression events could be higher given that the ABBA / BABA
427 test is not capable of testing introgression between sister lineages regardless of whether these
428 represent tip taxa, or ancestral sister branches deeper in the phylogeny. Sister lineages at the tips
429 of a phylogeny represent the most closely related pairs of taxa, are often geographically
430 proximate, and might thus be expected to experience the highest amounts of introgression.

Likewise, we analyzed relatively small datasets of SNPs (which ranged from 2030 to 6594 SNPs for each ABBA / BABA test; Table S2) which reduces our ability to detect introgression events involving a smaller proportion of the genome. With full genome sequences, significant geneflow was detected between Neandertal and Eurasian human lineages despite having small values of the *D* statistic (ranging from 0.027 to 0.058). All of our significant ABBA / BABA tests had absolute *D* statistics exceeding 0.23 (range 0.23 to 0.36). With full genome sequencing additional introgression events involving a much smaller genomic component might be supported. These considerations suggest that substantially more than five introgression events could have occurred in the history of this genus and indicate that introgression is likely to be a common phenomenon during diversification of Neotropical taxa such as *Dendrocincla*.

Our data suggest the time window when introgression is possible following divergence from a common ancestor ranges from zero to at least 2.5 million years (Myr) (Fig. 6A). One or two introgression events occurred less than a million years following divergence, consistent with introgression during the early stages of speciation.. In contrast, two introgression events occurred more than two million years following divergence (the oldest dating to 2.2 to 2.8 Myr between the ancestors of the *D. fuliginosa* and *D. merula* complexes), suggesting that gene flow is possible despite long periods for reproductive isolation to accumulate. These dates point to a protracted speciation process in the Neotropics in which reproductive isolation accumulates slowly and introgression across hybrid zones or over semi-permeable geographic barriers may be possible

We failed to detect introgression between *D. f. atrirostris* and *D. f. rufoolivacea* for which we previously described a hybrid zone (Weir et al. 2015). Our dating suggests this pair of subspecies diverged from a common ancestor ca. 3.1 Mya. The lack of evidence for introgression

454 despite localized hybridization at the contact zone suggests that taxa pairs of this age may have
455 exceeded the end of the time window when introgression remains possible. If indeed this is the
456 case, then the lack of evidence from the ABBA / BABA test for introgression would also suggest
457 that hybridization has likely not occurred during earlier time periods when reproductive isolation
458 would have been weaker, perhaps because these taxa only recently came into geographic contact
459 for the first time. We suggest that the time window of introgression in *Dendrocincla* ends
460 sometime between 2.5 and 3.1 million years following divergence. Detailed analyses of
461 Amazonian hybrid zones in another species pair of woodcreeper that diverged about 2.5 Mya and
462 a four million year old pair of antbirds likewise found that despite frequent hybridization and a
463 lack of strong premating isolation, the genome of these species pairs was essentially immune to
464 introgression due to near complete post-zygotic reproductive isolation (Pulido-Santacruz et al.
465 2018). Taxa may continue to form hybrid zones for some time after the time window of
466 introgression has closed without introgression ensuing.
467 The relationship between total reproductive isolation and time are predicted to differ for
468 different classes of reproductive isolation (e.g. (Gourbière and Mallet 2010). Due to their
469 epistatic nature, the accumulation of genetic incompatibilities (e.g. Dobzhasky-Muller
470 incompatibilities) are predicted to snowball – that is to increase faster than linear through time
471 (Orr 1995 p. 199; Orr and Turelli 2001; Matute et al. 2010; Moyle and Nakazato 2010) – and to
472 result in an approximately exponential decline in hybrid fitness. In contrast, the decrease in
473 hybrid fitness due to chromosomal rearrangements is predicted to be linear (e.g. no epistatic
474 chromosomal evolution; Gourbière and Mallet (2010) and sources therein), while the rate of
475 prezygotic isolation evolving under reinforcement is expected to slow down rather than speed up
476 because the strength of selection to reinforce assortative mating declines as the frequency of

hybridization declines (Gourbière and Mallet 2010). Interestingly, the proportion of the genome introgressed for the five cases of introgression and the one contemporary hybrid zone in *Dendrocincla* appears to decline exponentially with the age of the lineages at hybridization (Fig. 6B). This result mimics the snowballing effect expected if the accumulation of generic incompatibilities drives reproductive isolation. We caution that sample size is low (n=6) and that the non-linear nature of the data is largely driven by inclusion of the present-day hybrid zone between *D. f. atrirostris* and *D. f. rufoolivacea* across which introgression is essentially zero. If the relationship holds it would suggest that the genome becomes progressively less permeable to geneflow as the number of genetic incompatibilities increases, with genome permeability essentially dropping rapidly after about 2.5 million years since divergence. Alternatively, older lineages may have had more time for introgressed genes to be eliminated by purifying selection. However, a strong relationship between the proportion of the genome that has introgressed and the time of hybridization is lacking (Fig 6C), and it seems unlikely that purifying selection would operate over such long periods.

The geographic context of introgression is also an important consideration. Broad sympatric overlap provides the greatest geographic opportunity for hybridization, parapatry along narrow contact zones provides less opportunity, while allopatry provides limited opportunity. Two of the five introgression events occurred between clades which are currently sympatric over a 500 km North-to-South stretch of Nicaragua and Honduras (between *D. anabatina* and the ancestor of a clade including *D. f. ridgwayi*, *D. f. meruloides* and *D. f. neglecta*) and over most of the Amazon basin (between the ancestor of the *D. fuliginosa* and the ancestor of the *D. merula* clades). In both cases, introgression appears to have involved an ancestral taxon during an earlier

time period when geographic overlap may not yet have been attained. As such, we have no solid evidence for introgression following attainment of broad sympatry, though introgression during a sympatric state remains possible. While sympatry maximizes geographic opportunity for hybridization, species which are broadly sympatric likely exhibit strong levels of reproductive isolation, without which they likely could not persist in sympatry. Introgression involving substantial proportions of the genome are generally unlikely for species which have attained broad sympatry, though exceptions are documented (e.g. Blue-winged / Golden winged warblers, Toews et al. (2016); Capuchinos, Campagna et al. (2017)).

Surprisingly, we failed to find any convincing cases of introgression involving currently parapatric taxa. Parapatric taxa often form hybrid zones where they come in contact which might provide an ideal opportunity for introgression, though the sole known hybrid zone in *Dendrocincla*, which we discussed above, showed no evidence of introgression using ABBA / BABA tests. Other notable examples of extensive parapatry in *Dendrocincla* failed to show significant ABBA / BABA tests (e.g. *D. f. neglecta* and *D. f. atrirostris*). We did not detect introgression between *D. tyrannina* and *D. merula* which replace each other elevationally along most of the transition between the Andes and Amazon from Colombia to Bolivia, albeit with a slight elevational gap between their ranges. Elevational differentiation may have helped to prevent introgression in this case.

Rivers often occur along the contact zones between Amazonian taxa (Haffer 1969, 1997) and may be an important driver of speciation (Haffer 1997; Naka et al. 2012; Ribas et al. 2012; Naka and Brumfield 2018). Rivers may prevent gene flow in which case taxa on opposite sides of these barriers could be considered allopatric, or they may be permeable to gene flow in which case taxa should be considered parapatric. We tested for intraspecific introgression between

523 subspecies of *D. merula* (*D. m. obidensis* and *D. m. castanoptera*; *D. m. obidensis* and *D. m.*
524 *olivascens*) and within *D. fuliginosa* (between *D. f. fuliginosa and D. f. atrirostris*) which were
525 fully separated by the main Amazon River. None of these comparisons were significant. This
526 suggests that the Amazon river may be impermeable to gene flow or that if dispersal across this
527 barrier does occur, then it is sufficiently rare that it is not detectable by the ABBA/BABA tests
528 implemented on our dataset. Our results are consistent with rivers acting as drivers of speciation
529 in which cross-river gene flow is limited.
530 While many high latitude species of birds are migratory and may accidentally wander into
531 the breeding ranges of allopatric congeners, potentially leading to introgression between
532 allopatric populations, woodcreepers and most other Neotropical passerine species tied to tropical
533 forest show limited if any tendency to wander geographically. As such, introgression between
534 fully allopatric taxa may be highly unlikely. Nevertheless, of the five introgression events we
535 document, three occurred between allopatric taxa. In two of these cases, it seems likely that
536 geographic ranges of currently allopatric taxa met during past wetter periods of forest expansion.
537 For example, introgression between the Atlantic forest (*D. turdina*) and south-central Amazonia
538 (*D. fuliginosa atrirostris*) was strongly supported. Both regions are widely separated by xeric
539 forests and open habitats of the Argentinean and Paraguayan Chaco, the Cerrado and the
540 Caatinga in north-eastern Brazil (Ab'Saber 1977). Palynological evidence suggests that these
541 were connected in the past through gallery forests that expanded into the Chaco, Cerrado and
542 Caatinga along two main routes (Ledru 1993; Behling 1998, 2002; Wang et al. 2002). A southern
543 route connected the Amazon forests to the southern Atlantic Forest through the Chaco in
544 Argentina, Bolivia and Paraguay, while a second northern route connected the northern Atlantic
545 Forest through the Caatinga in northeastern Brazil. Comparative phylogenetic studies across

546 distinct co-distributed taxa (e.g. in birds: Batalha-Filho et al. 2013, mammals: Costa 2003, and
547 amphibians: Fouquet et al. 2012) have provided additional evidence for both routes. Our results
548 support introgression only via the southern Chaco corridor (e.g. Atlantic forest *D. turdina*
549 introgressed with south-central Amazonian *D. f. atrirostris*). The presence of distinct crown
550 streaking in *D. f. atrirostris* had led previous authors to place it within *D. turdina* (see Hoyo et al.
551 2003), which also has a streaked crown, and could represent a character that has introgressed
552 from the Atlantic Forest to the Amazon via this route. We date this introgression event to 2.0 to
553 2.8 Mya suggesting that wet forest connections may have existed prior to the major glacial cycles
554 of the mid to late Pleistocene. In contrast, we found no evidence of introgression between the
555 Atlantic forest and south-eastern Amazonia along the northern route (e.g. no gene flow between
556 *D. turdina* and the south-eastern Amazonian *D. f. rufoolivacea*).
557 We also found support for introgression between the currently allopatric *D. f. ridgwayi*
558 found in the Choco region through Central America and *D. f. meruloides* of northern Venezuela
559 and Trinidad sometime during the past 300 kya. We did not sample the geographically
560 intervening *D. f. lafresnayei* of northern Colombia and Venezuela (whose range closely
561 approaches that of *D. f. meruloides* in northern Venezuela and *D. f. ridgwayi* in Colombia).
562 However, a recent phylogeographic analysis using mitochondrial DNA suggested that *D. f.*
563 *lafresnayei* may not be a valid subspecies, with the western part of its range nested within *D. f.*
564 *ridgwayi* and the eastern half forming a monophyletic clade together with *D. f. meruloides, D. f.*
565 *deltana,* and *D. f. barinensis* (Schultz et al. 2019). Introgression thus appears to have involved
566 lineages which currently approach each other geographically in northern Columbia, and contact
567 between these lineages during a wetter past interglacial period would not be unexpected.

In contrast to the above two cases where past geographic contact between currently allopatric taxa seems likely, we found one case of introgression between geographically distant allopatric taxa. Evidence of introgression between *D. f. rufoolivacea* of SE Amazonia and the ancestor of *D. f. neglecta* (western and northern Amazonia) and *D. f. meruloides* (northern Venezuela and Trinidad) is hard to explain because *D. f. rufoolivacea* is currently geographically separated from the other subspecies by the ranges of *D. f. atrirostris* and *D. f. fuliginosa* (Fig. 1). Whether this introgression event resulted from long distance leapfrog dispersal across the ranges of the intervening subspecies or occurred during a glacial cycle (i.e. the event is dated to the mid Pleistocene) when the range distributions of these subspecies may have had a different configuration that resulted in geographic contact, is hard to determine. The Tapajos, Madeira and other rivers in Amazonia – which often form the boundaries between geographically adjacent taxa – may have shifted their drainage patterns periodically through the Pleistocene (Hayakawa and Rossetti 2015; Ruokolainen et al. 2018) resulting in the current allopatry between taxa which were once in contact and able to introgress. Interestingly, our sample included three individuals of *D. f. neglecta* that occurred on the eastern bank of the Madeira River (MPDS 616, 748, and 749 representing the first record of this taxon on the eastern bank) within the Aripaunã-Machado mini-interfluve. The presence of *D. f. neglecta* on the eastern bank of the Madeira may indicate a former connection once occurred in this region to the east. Biogeographic ties between this mini-interfluve and the region east of the Tapajos river have previously been suggested for *Lepidothrix* manakins in which introgression may have occurred from the eastern *L. iris iris* into the local population of *L. nattereri* from Aripaunã -Machado (Dias et al. 2018).

We have already discussed the limitation that the ABBA / BABA test is not capable of testing introgression between sister taxa, and thus, likely underestimates the number of

591 introgression events. Another issue is that the *D*-statistic may be extreme if small windows of
592 sampled SNPs are investigated, mainly due to the presence of a rather limited amount of unlinked
593 information (Martin et al. 2015). To avoid this, we analyzed a genome-wide sample of SNPs (see
594 methods) with a minimum of 2,030 SNPs for each four-taxon comparison, and we retained SNPs
595 which were at least 10 kbp apart to help ensure that SNPs were not closely linked. Though the
596 draft reference genome we used lacks chromosome information, it is likely that these SNPs are
597 derived from across the genome rather than from a single genomic region.

598 Another issue is that significant ABBA/BABA tests might reflect parallel natural
599 selection rather than introgression. Parallel natural selection acting on the P3 and either the P1 or
600 the P2 taxa could result in an excess of ABBA or BABA patterns, even in the absence of gene
601 flow between them (Durand et al. 2011). The levels of excess measured here for the significant
602 comparisons range from 37 to 95, but the actual number of loci affected for the entire genome
603 would conceivably be much higher given that our filtered GBS dataset only targets a small
604 fraction of the genome (less than 1%). Whether parallel selection would affect this number of
605 SNPs is difficult to assess. However, parallel selection would be most likely for broadly
606 sympatric taxa that occupy similar environments, and only two of our introgression events
607 involved taxa which currently are sympatric.

608

609 **Conclusions**

610 Hybridization has long been considered a negative process to species diversification, reducing
611 genetic diversity through introgression. Yet, an increasing number of documented cases have
612 recently shown that introgression is prevalent in invertebrates, aquatic vertebrates or island

radiations from the Neotropics (e.g. Mallet et al. 2007; Cui et al. 2013; Martin et al. 2013; Schumer et al. 2013; Grant and Grant 2014; Merot et al. 2017). Our analyses suggest that introgression was also fairly common within a continental radiation of terrestrial vertebrates from the Neotropics. We uncovered historical introgression events among closely and distantly related lineages of *Dendrocincla*, some of which diverged more than 7 million years ago (Weir & Price 2011a), suggesting that hybridization was present throughout the evolutionary history of the group. Our analyses support introgression events within 2.5 million years following divergence suggesting that introgression is possible even between moderately old taxa. Despite this long window when introgression is possible, we found an approximately exponential decline in the proportion of the genome introgressing with increasing time between divergence and introgression, potentially consistent with the accumulation of genetic incompatibilities which progressively render greater amounts of the genome immune from introgression until introgression ceases and "genomic speciation" (*sensu* Gompert et al. 2017) is achieved. These results are in agreement with a growing list of studies suggesting that reproductive isolation in Amazonian and other Neotropical birds develops over an extended timeframe (Martin et al. 2010; Weir and Wheatcroft 2011; Weir et al. 2012, 2015; Pulido-Santacruz et al. 2018) allowing for ample opportunities for introgression – often involving substantial amounts of the genome as documented here – during the diversification process.

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858 **Table 1.** Twelve significant ABBA / BABA tests (for which $p < 0.005$) which we interpret as representing five distinct
859 introgression events. All seven members of the *D. fuliginosa* / *D. anabatina* clade when placed as P3 tested positive for
860 introgression with the ancestor of the *D. merula* clade. We interpret this as a single introgression event represent the ancestor of
861 *D. fuliginosa* into the ancestor of *D. merula.* Likewise, both subspecies of *D. turdina* when placed as P3 tested significant for
862 introgression with *D. f. atrirostris* which we interpret as a single introgression event involving the ancestor of *D. turdina.* The
863 last column denotes gene flow events colour coded in Figure 5. *D* represents the *D* statistic and SE is the standard error. f_{hom} is
864 an estimate of the proportion of the genome introgressing.
865
866

P1	P2	P3	SNPs	ABBA	BABA	*D*	SE of *D*	*p-value*	f_{hom}	Ingression event
D. f. meruloides	*D. f. neglecta*	*D. f. ridgwayi*	3754	57	95	-0.250	0.0787	0.0015	0.110	Blue
Branch I (D. f. meruloides)	*D. f. ridgwayi*	*D. f. rufoolivacea*	4416	36	78	-0.368	0.0869	<0.00003	0.079	Yellow
branch J (D. f. meruloides)	*D. f. rufoolivacea*	*D. a. typhia*	3684	63	113	-0.284	0.0723	<0.00009	0.093	Turquoise
branch M (D. f. meruloides)	*D. f. atrirostris*	*D. t. turdina*	2773	89	54	0.245	0.0815	0.0027	0.065	Pink
branch M (D. f. meruloides)	*D. f. atrirostris*	*D. t. taunayi*	5904	206	111	0.300	0.0534	<0.00001	0.089	Pink
branch D	*D. tyrannina*	*D. f. atrirostris*	4717	83	133	-0.231	0.0655	0.0004	0.051	Purple

(D. m. obidensis)										
branch D (D. m. obidensis)	*D. tyrannina*	*D. a. typhia*	3646	72	109	-0.204	0.0729	0.005	0.047	Purple
branch D (D. m. obidensis)	*D. tyrannina*	*D. f. fuliginosa*	3714	57	99	-0.269	0.0773	0.0005	0.058	Purple
branch D (D. m. obidensis)	*D. tyrannina*	*D. f. rufoolivacea*	4000	63	107	-0.259	0.0740	0.0005	0.055	Purple
branch D (D. m. obidensis)	*D. tyrannina*	*D. f. ridgwayi*	4120	71	115	-0.237	0.0716	0.001	0.052	Purple
branch D (D. m. obidensis. CN541)	*D. tyrannina. FM429946*	*D. f. neglecta*	3308	54	94	-0.270	0.0787	0.0006	0.060	Purple
branch D (D. m. obidensis)	*D. tyrannina*	*D. f. meruloides*	4067	65	121	-0.301	0.0698	0.00002	0.065	Purple

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FIGURES LEGENDS

Figure 1. Geographic range of *Dendrocincl*a species and subspecies and sampling localities. Borders between subspecies are approximate. Sample localities (Table S1 in supporting information) are shown by black circles. Major Amazonian rivers shown by blue lines. Ranges adapted from Weir and Price 2011b.

Figure 2. Illustrative example for the ABBA/BABA test to quantify introgressive gene flow between lineages in a four-taxon phylogeny (P1, P2, P3 and Outgroup). ABBAs and BABAs are SNPs at which either P2 and P3 shared the derived allele "B" (ABBA) or P3 and P1 (BABA) shared the derived allele "B". The red line represents two possible origins of the derived allele through sorting of ancestral polymorphism. ABBAs and BABAs should occur with equal frequency if derived solely through the sorting of ancestral polymorphism. Alternatively, significant differences of the number of ABBA versus BABA sites suggests introgression. The illustrated example had a significant excess of ABBA's suggesting gene flow between P3 (*Dendrocincla fuliginosa ridgwayi*) and P2 (*D. f. neglecta*) shown by black arrows, but does not indicate whether gene flow was bidirectional, or unidirectional from P3 into P2 or from P2 into P3. As implemented here, P1 is fully allopatric to P3, while P2 and P3 are in close geographic contact (either sympatric or parapatric, see main text for details). Bird illustrations are reproduced as they are in Handbook of the Birds of the World Alive with the permission of HBW Alive Lynx Edicions Barcelona.

889 **Figure 3**. Example implementation of the ABBA / BABA test. A) Phylogeny of five species eight
890 ABBA / BABA tests are applied in such a way as to test for introgression between both lineages
891 that terminate at the tips of the phylogeny in extant taxa (numbered 1 to 5) as well as past lineages
892 that occupy interior positions of the phylogeny (labelled A1 to A3). Introgression can be tested
893 between most lineages but cannot be tested between sister lineages (e.g. 2 and 3; 4 and 5; 1 and
894 A1; A2 and A3). Tests in which interior lineage A1 is placed in a P2 position can use either tip
895 lineage 1 or 2 to represent it assuming no introgression has occurred into lineage 1 or 2. If
896 introgression has occurred into lineage 1, then lineage 2 should be used to represent lineage A1
897 and introgression has occurred into lineage 2 then lineage 1 should be used to represent lineage
898 A1. B) If introgression is supported from multiple P3 lineages that together make up a clade (e.g.
899 lineages 1 to 3) into the same P2 or P1 lineage (e.g. lineage 4), then we assume the most
900 parsimonious reconstruction of a single introgression event (shown by thick arrow) that involved
901 the ancestral lineage preceding the clade of P3 species (e.g. lineage A2) rather than multiple
902 introgression events (thin arrows). With this assumption it is possible to test for introgression
903 involving many ancestral lineages. It is also possible to provide date ranges for introgression
904 events. In the example in panel B, we can date the introgression event as having occurred after the
905 node following lineage A3 at 6 Mya and before the node following lineage A2 at 5.5 Mya.

906

907 **Figure 4.** Maximum likelihood phylogeny estimated in IQ-Tree using 24,130 SNPs and 1,000
908 bootstrap replicates to indicate nodal support above branches. Tissue, field number or museum
909 catalog number follows the taxon name.

Figure 5. Phylogenetic relationships among *Dendrocincla* taxa. Majority-rule consensus species tree from SVDQuartets using 24,130 SNPs. The numbers above the branches are non-parametric bootstrap values for nodal support which are shown only for nodes with less than 100% support. Ages of nodes were estimated using the multigene coalescent from the program G-PhoCS. Arrows denote significant gene flow events ($p < 0.005$) and point from the P3 species to the P1 or P2 species. The direction of the arrow does not imply introgression occurs in only this direction, though introgression from the P3 to the P1/P2 species is more likely (Martin et al. 2015). Circles show the nodes in which daughter lineages experienced introgression. Letters A to Q indicate internal branches also used in ABBA / BABA testing and referenced in Table 1 and S2.

Figure 6. The timing and magnitude of introgression events in *Dendrocincla* woodcreepers. A) Lineage age at hybridization (vertical bars indicate lower and upper estimates), time of hybridization (horizontal bars indicate lower and upper estimates). B) Relationship between the proportion of the genome introgressing (f_{hom}) and the lineage age at introgression (using the midpoint of the estimate). The black line in B shows the best fit exponential decay curve ($f_{hom} = 0.12 + 0.0045(1\text{-}exp(t))$ fit to the midpoint estimates of lineage age at introgression. The black line in B shows the best fit linear relationship ($f_{hom} = 0.069 + 0.00027x$, where x = time of hybridization). Colours of introgression events correspond to those in Fig 5. The red dot represents *D. fuliginosa atrirostris* and *D. f. rufoolivacea* which, despite currently possessing a hybrid zone, did not produce a significant ABBA/BABA test and whose f_{hom} was estimated to be less than 0.01.

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Table S1. List of *Dendrocincla* samples used in this study.

	Taxon	Institution	Tissue or field number: museum catalog number	Locality
1	*D. tyrannina*	LSUMZ	12108	Ecuador, Pichincha, Mindo
2	*D. tyrannina*	FMNH	429946	Peru, Cuzco, Paucartambo, Pillahuata
3	*D. merula merula*	KU	1184: 88668	Guyana, Iwokrama Reserve, Kurupukari, ca 41 road km SW
4	*D. merula merula*	KU	1307: 88767	Guyana, Iwokrama Reserve, W bank Essequibo River, ca 72 river km SW Kurupukari
5	*D. merula obidensis*	MPEG	CN 541: 65374	Brazil, Pará, Alenquer, ESEC Grão-Pará (00°09' S; 55°11' W)
6	*D. merula barletti*	FMNH	JGT 009: 391082	Bolivia, La Paz, T C O Campamento Araona, Palmasola, Rio Manupari
7	*D. merula barletti*	MVZ	5077: 169483	Peru, Madre de Dios, Alberque, Rio Madre de Dios, 12 km E Puerto Maldonado
8	*D. merula barletti*	FMNH	JGT 035: 391084	Bolivia, El Beni, Hacienda Los Angeles, 10 km E Riberalta
9	*D. merula olivascens*	MPEG	MPDS 0810: 60949	Brazil, Pará, Juruti, Projeto Juruti/Alcoa, Acampamento Mutum (02°36 'S; 56°11' W)
10	*D. merula olivascens*	MPEG	TLP B 262: 69340	Brazil, Mato Grosso, Paránaíta, margem esquerda Rio Paránaíta, Fazenda Aliança (09°33' 46.0" S; 56° 45' 40.8" W)
11	*D. merula castanoptera*	MPEG	PPS 167: 74916	Brazil, Pará, Altamira, Fazenda Ipiranga (S -9,26355; W -54,46849)
12	*D. merula castanoptera*	MPEG	PPS 060: 74809	Brazil, Mato Grosso, Peixoto de Azevedo, Fazenda Pium (S- 10,50355 ; W -54,39682)
13	*D. merula castanoptera*	MPEG	PPS 122: 74871	Brazil, Mato Grosso, Matupa, Fazenda São Jerônimo, Cachimbo (S- 10,34717 ; W -54,73693)
14	*D. merula castanoptera*	MPEG	PPS 239: 74987	Brazil, Mato Grosso, Feliz Natal, ENA Settlement (S -12,10803 ; W -54,31233)
15	*D. merula castanoptera*	MPEG	a8264	Brazil, Pará, Belterra, Flona do Tapajós, Km 117 BR163
16	*D. merula castanoptera*	-	MSF 082	Brazil, Mato Grosso, Matupa, Fazenda Sao Jeronimo, Cachimbo
17	*D. merula castanoptera*	MPEG	PPS 134: 74883	Brazil, Mato Grosso, Matupa, Fazenda São Jerônimo, Cachimbo (S -10,34521 ;W -54,73592)
18	*D. merula castanoptera*	MPEG	MSF 068: 74601	Brazil, Mato Grosso, Matupa, Fazenda São Jerônimo (S -10,28368 ;W -54,67801)
19	*D. merula castanoptera*	MPEG	PPS 212: 74961	Brazil, Mato Grosso, Guarantã do Norte, Fazenda São Jorge (S -10,12599; W -54,36266)
20	*D. merula castanoptera*	FMNH	SA 008: 391305	Brazil, Pará, Serra dos Carajas
21	*D. merula badia*	MPEG	FCR 038: 58961	Brazil, Pará, Tailândia, Fazenda Rio Capim, CIKEL (3° 42' 15.2" S; 48° 33' 45" W)

22	*D. homochroa ruficeps*	STRI	MJM 0671	Panama, Cerro Azul
23	*D. homochroa ruficeps*	STRI	MJM 8576	Panama, Darién, Chucanti
24	*D. homochroa homochroa*	KU	2192: 89392	Mexico, Campeche, Silvituc, 20 km S
25	*D. homochroa homochroa*	KU	4877: 94159	El Salvador, Ahuachapan, Municipio San Francisco Menendez, Parque Nacional El Imposible, Sector La Fincona
26	*D. homochroa acedesta*	STRI	MJM 7718	Panama, Comarca Ngäbe-Buglé
27	*D. homochroa acedesta*	STRI	MJM 9219	Panama, Comarca Ngäbe-Buglé
28	*D. turdina turdina*	KU	3783: 91228	Paráguay, Caazapa/Itapua, San Rafael N.P., Parábel
29	*D. turdina turdina*	MPEG	CC 2862	Unknown
30	*D. turdina taunayi*	FMNH	SAC 297: 399178	Brazil, Alagoas
31	*D. turdina taunayi*	FMNH	SAC 314: 399180	Brazil, Alagoas
32	*D. turdina taunayi*	FMNH	SAC 307: 399179	Brazil, Alagoas
33	*D. turdina taunayi*	FMNH	USG 381: 399183	Brazil, Alagoas, Ibateouara, Envenho Ceimba, Usina Serra Grande
34	*D. turdina taunayi*	FMNH	USG 335: 399181	Brazil, Alagoas, Ibateouara, Envenho Ceimba, Usina Serra Grande
35	*D. turdina taunayi*	FMNH	USG 380: 399182	Brazil, Alagoas, Ibateouara, Envenho Ceimba, Usina Serra Grande
36	*D. fuliginosa atrirostris*	MPEG	PPS 293: 75039	Brazil, Mato Grosso, Santiago do Norte, Fazenda Prezzoto (S -13,12606; W -54,42907)
37	*D. fuliginosa atrirostris*	MPEG	JTW 1103 75137	Brazil, Mato Grosso, Nova Mutum, south of Nova Mutum (S -14.15006; W -56.09396)
38	*D. fuliginosa atrirostris*	MPEG	JTW 1171: 75203	Brazil, Mato Grosso, Peixoto de Azevedo, Fazenda Pium (S -10,50329; W -54,39640)
39	*D. fuliginosa atrirostris*	MPEG	PPS 362: 75105	Brazil, Mato Grosso, Marcelândia, Fazenda Golin (S -11,26562; W -54,72123)
40	*D. fuliginosa atrirostris*	MPEG	MT 078: 70218	Brazil, Mato Grosso, Querência, Fazenda Tanguro (12° 53' 29,5" S; 52° 22' 26" W)
41	*D. fuliginosa atrirostris*	MPEG	AMANA 086: 65615	Brazil, Pará, Itaituba, FLONA Amaná, margem direita, Igarapé Montanha (4° 52' 55,9 "S; 56° 58' 07,0" W)
42	*D. fuliginosa atrirostris*	MPEG	FPR 083: 67011	Brazil, Amazonas, Maués, Flona do Pau Rosa, Comunidade Sta. Teresa (03° 54' 52" S; 58° 17' 41" W)
43	*D. fuliginosa atrirostris*	MPEG	FPR 072: 67030	Brazil, Alagoas, Maués, Flona do Pau Rosa, Comunidade São Tomé (03° 54' 25,2" S; 58° 24' 06,5" W)
44	*D. fuliginosa atrirostris*	FMNH	391074	Bolivia, La Paz, T C O Campamento Araona, Palmasola, Rio Manupari
45	*D. fuliginosa atrirostris*	MPEG	AMANA 010: 65116	Brazil, Pará, Itaituba, FLONA Amanã, margem direita Igarapé Montanha (4° 52' 58,7" S; 56° 58' 10,1" W)

46	*D. fuliginosa atrirostris*	MPEG	JTW 1374: 75405	Brazil, Mato Grosso, Sinop, Faz. Missioneira (S -11.59762, W -55.66064)
47	*D. fuliginosa atrirostris*	FMNH	391076	Bolivia, El Beni: Hacienda Los Angeles, 10 km E Riberalta
48	*D. fuliginosa atrirostris*	FMNH	391075	Bolivia, La Paz, T C O Campamento Araona, Palmasola, Rio Manupari
49	*D. fuliginosa atrirostris*	MPEG	MT 067: 70215	Brazil, Mato Grosso, Querência, Fazenda Tanguro (13° 03' 46" S; 52° 22' 51,7" W)
50	*D. fuliginosa atrirostris*	FMNH	429948	Peru, Cuzco, Paucartambo, San Pedro
51	*D. fuliginosa atrirostris*	FMNH	391078	Bolivia, La Paz, T C O Campamento Araona, Palmasola, Rio Manupari
52	*D. fuliginosa atrirostris*	FMNH	391077	Bolivia, El Beni, Hacienda Los Angeles, 10 km E Riberalta
53	*D. fuliginosa fuliginosa*	KU	1241: 88769	Guyana, Iwokrama Reserve, Kurupukari, ca 41 road km SW (4.3333333 , -58.8500000)
54	*D. fuliginosa fuliginosa*	KU	5752: 94825	Guyana, E Barima River, along Washikura River (8.2500000, -59.7333333)
55	*D. fuliginosa fuliginosa*	KU	5780: 94823	Guyana, E Barima River, along Washikura River (8.2500000, -59.7333333)
56	*D. fuliginosa fuliginosa*	FMNH	391298	Brazil, Amapa
57	*D. fuliginosa fuliginosa*	FMNH	391302	Amapa, Tartarugalzinho, Fazenda Sao Bento
58	*D. fuliginosa fuliginosa*	FMNH	391299	Brazil, Amapa
59	*D. fuliginosa fuliginosa*	FMNH	391300	Brazil, Amapa
60	*D. fuliginosa rufoolivacea*	MPEG	MSF 261: 78343	Brazil, Pará, Anapu, Fazenda do Raimundo (S -3.15230, W -51.60348)
61	*D. fuliginosa rufoolivacea*	MPEG	PIME 231: 69018	Brazil, Pará, Altamira, Flona do Trairão (04°36'31,5" S; 55°29'47,6" W)
62	*D. fuliginosa rufoolivacea*	MPEG	MSF 222: 78305	Brazil, Pará, Pacajá, Fazenda Sr. Zé Mário (S -3.79746; W -50.70790)
63	*D. fuliginosa rufoolivacea*	MPEG	PIME 042: 67187	Brazil, Pará, Itaituba, Flona Itaituba II, Capãozinho
64	*D. fuliginosa rufoolivacea*	MPEG	PPS 188: 74937	Brazil, Pará, Altamira, Fazenda Ipiranga (S -9,26392; W -54,46769)
65	*D. fuliginosa rufoolivacea*	MPEG	PPS 137: 74886	Brazil, Mato Grosso, Guarantã do Norte, 63km East Guaranta do Norte (S -9,94184; W -54,34259)
66	*D. fuliginosa rufoolivacea*	MPEG	PPS 187: 74936	Brazil, Mato Grosso, Altamira, Fazenda Ipiranga (S -9,26392; W -54,46769)
67	*D. fuliginosa rufoolivacea*	MPEG	PIME 016: 66112	Brazil, Pará, Belterra, Flona do Tapajós, Br 163 km 17

68	*D. fuliginosa rufoolivacea*	MPEG	PIME 112: 67636	Brazil, Pará, Belterra, Fazenda Treviso, margem esquerda Igarapé Moju (S -3.47294; W -54.56546)
69	*D. fuliginosa meruloides*	STRI	TRDFU 1	Trinidad, Simla Research Station
70	*D. fuliginosa meruloides*	STRI	TRDFU 10	Trinidad, Hollis Reservoir
71	*D. fuliginosa neglecta*	MPEG	JAP 096: 62603	Brazil, Amazonas, Japurá, Rio Mapari (02° 02' 59,6" S; 67° 15' 47,1" W)
72	*D. fuliginosa neglecta*	MPEG	CUJ 160: 60136	Brazil, Amazonas, RDS Cujubim, margem E Rio Jutaí (04° 39' 14" S; 68° 19' 38" W)
73	*D. fuliginosa neglecta*	MPEG	MAD 016: 73253	Brazil, Rondônia, Porto Velho, Cujubim, margem oeste Rio Madeira (08° 33' 35,4" S; 63° 37' 35,4" W)
74	*D. fuliginosa neglecta*	MPEG	PUC 185: 57024	Brazil, Amazonas, Tefé, Base Petrobras/Urucu, Papagaio (04° 51' S; 65° 04' W)
75	*D. fuliginosa neglecta*	MPEG	MPDS 616: 58680	Brazil, Amazonas, Município de Humaitá, T. Indígena Parintintin, Aldeia Pupunha (07° 28' S; 62° 56' W)
76	*D. fuliginosa neglecta*	MPEG	MPDS 748: 59015	Brazil, Amazonas, Humaitá, Território Indígena Ipixuna, Aldeia Canavial, Miriti (06° 33' S; 62° 03' W)
77	*D. fuliginosa neglecta*	MPEG	MPDS 749: 59014	Brazil, Amazonas, Humaitá, Território Indígena Ipixuna, Aldeia Canavial, Miriti (06° 33' S; 62° 03' W)
78	*D. fuliginosa ridgwayi*	STRI	GMS 1111	Panama: Coclé Prov, El Valle, Foothills NE of town
79	*D. fuliginosa ridgwayi*	STRI	JK 04254	Panama: Coclé Prov, El Valle, Foothills NE of town
80	*D. fuliginosa ridgwayi*	STRI	IJL 064	Panama, Bocas del Toro, Cerro Chalite
81	*D. fuliginosa ridgwayi*	STRI	JTW 172	Panama, Bocas del Toro, above Chiriqui Grande
82	*D. fuliginosa ridgwayi*	STRI	JTW 206	Panama, Bocas del Toro; Valle de Risco (N 09°13',19.5"; W082°24'39.5")
83	*D. fuliginosa ridgwayi*	STRI	JTW 269	Panama, Bocas del Toro; Valle de Risco (N 09°13',19.5"; W 082°24'39.5")
84	*D. fuliginosa ridgwayi*	STRI	JTW 744	Panama, Darien, Puerto Pina
85	*D. anabatina typhla*	KU	536: 89394	Mexico, Quintana Roo, Puerto Morelos, Jardin Botanico (20.8333333 , -86.9000000)
86	*D. anabatina typhla*	KU	565	Mexico, Quintana Roo, Puerto Morelos, Jardin Botanico (20.8333333 , -86.9000000)
87	*Deconychura longicauda*	MPEG	JTW 1323: 75355	Brazil, Mato Grosso, Feliz Natal, ENA Settlement (S -12.10803; W 54.31233)

Table S2. ABBA / BABA comparisons. *D* represents the *D* statistic and SE is the standard error. Z is the number of standard deviations from 0 (the expected value) for *D*. Significance was assessed for each replicate by converting the Z-score into a two tailed p-value, and using 0.005 as a conservative cutoff for significance. For species voucher information see Table S1.

#	P1	P2	P3	OUTGROUP	SITES	ABBA	BABA	*D*	Z	SE *D*	*p*
1	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. tyrannina FM429946*	*D. longicauda*	3289	22	15	NA	NA	NA	NA
2	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. m. castanoptera PPS167*	*D. longicauda*	4021	31	20	NA	NA	NA	NA
3	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. m. badia FCR038*	*D. longicauda*	3491	25	21	NA	NA	NA	NA
4	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. m. obidensis CN541*	*D. longicauda*	3610	23	25	NA	NA	NA	NA
5	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. m. olivacens MPDS0810*	*D. longicauda*	2817	25	17	NA	NA	NA	NA
6	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. m. bartletti FM391084*	*D. longicauda*	3667	29	21	NA	NA	NA	NA
7	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. h. homochroa KU2192*	*D. longicauda*	3446	33	20	NA	NA	NA	NA
8	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. h. ruficeps MJM8576*	*D. longicauda*	3927	36	26	NA	NA	NA	NA
9	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. h. acedesta MJM9219*	*D. longicauda*	3955	37	25	NA	NA	NA	NA
10	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. turdina KU3783*	*D. longicauda*	2030	21	22	NA	NA	NA	NA
11	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. t. taunayi FM399181*	*D. longicauda*	3960	37	39	NA	NA	NA	NA
12	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. f. atrirostris PPS293*	*D. longicauda*	4083	72	45	0.230769231	2.577461835	0.08953352	0.009952887
13	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. a. typhia KU536*	*D. longicauda*	3098	47	44	NA	NA	NA	NA
14	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. f. fuliginosa KU1241*	*D. longicauda*	2994	41	36	NA	NA	NA	NA
15	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. f. rufoolivacens MSF261*	*D. longicauda*	3509	50	57	-0.065420561	0.676726138	0.096672135	0.498579729
16	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. f. ridgwayi JK04254*	*D. longicauda*	3754	57	95	-0.25	3.178451161	0.078654661	0.001480642
17	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. tyrannina FM429946*	*D. longicauda*	4283	27	22	NA	NA	NA	NA
18	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. m. castanoptera PPS167*	*D. longicauda*	5351	37	38	NA	NA	NA	NA
19	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. m. badia FCR038*	*D. longicauda*	4301	32	32	NA	NA	NA	NA
20	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. m. obidensis CN541*	*D. longicauda*	4480	27	33	NA	NA	NA	NA
21	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. m. olivacens MPDS0810*	*D. longicauda*	3596	26	21	NA	NA	NA	NA
22	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. m. bartletti FM391084*	*D. longicauda*	4815	30	30	NA	NA	NA	NA
23	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. h. homochroa KU2192*	*D. longicauda*	4490	34	31	NA	NA	NA	NA
24	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. h. ruficeps MJM8576*	*D. longicauda*	5155	34	36	NA	NA	NA	NA
25	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. h. acedesta MJM9219*	*D. longicauda*	5191	34	39	NA	NA	NA	NA
26	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. turdina KU3783*	*D. longicauda*	2479	26	24	NA	NA	NA	NA
27	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. t. taunayi FM399181*	*D. longicauda*	5193	41	43	NA	NA	NA	NA
28	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. f. atrirostris PPS293*	*D. longicauda*	5533	60	65	-0.04	0.443566259	0.090178185	0.657356205
29	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. a. typhia KU536*	*D. longicauda*	4003	67	59	0.063492063	0.70996703	0.089429594	0.477724582
30	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. f. fuliginosa KU1241*	*D. longicauda*	3937	46	57	-0.106796117	1.084675507	0.098459047	0.2780654

31	*Branch I (D. f. meruloides TRDFU11)*	*D. f. ridgwayi JK04254*	*D. f. rufoolivacens MSF261*	*D. longicauda*	4416	36	78	-0.368421053	4.237295647	0.086947214	2.26E-05
32	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. tyrannina FM429946*	*D. longicauda*	3711	24	30	NA	NA	NA	NA
33	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. m. castanoptera PPS167*	*D. longicauda*	4329	28	39	NA	NA	NA	NA
34	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. m. badia FCR038*	*D. longicauda*	3262	23	33	NA	NA	NA	NA
35	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. m. obidensis CN541*	*D. longicauda*	3679	28	32	NA	NA	NA	NA
36	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. m. olivacens MPDS0810*	*D. longicauda*	3073	20	29	NA	NA	NA	NA
37	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. m. bartletti FM391084*	*D. longicauda*	3959	21	36	NA	NA	NA	NA
38	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. h. homochroa KU2192*	*D. longicauda*	3645	33	37	NA	NA	NA	NA
39	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. h. ruficeps MJM8576*	*D. longicauda*	3902	39	43	NA	NA	NA	NA
40	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. h. acedesta MJM9219*	*D. longicauda*	3921	39	41	NA	NA	NA	NA
41	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. turdina KU3783*	*D. longicauda*	2205	23	28	NA	NA	NA	NA
42	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. t. taunayi FM399181*	*D. longicauda*	4202	48	47	NA	NA	NA	NA
43	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. f. atrirostris PPS293*	*D. longicauda*	4310	66	62	0.03125	0.352769941	0.088584645	0.72426092
44	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. a. typhia KU536*	*D. longicauda*	3249	67	70	-0.02189781	0.25533118	0.085762382	0.798467319
45	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. f. ridgwayi JK04254*	*D. longicauda*	3726	65	92	-0.171974522	2.202541653	0.078080032	0.02762707
46	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. f. neglecta CUJ160*	*D. longicauda*	2918	60	75	-0.111111111	1.29565329	0.085756824	0.195094961
47	*D. f. fuliginosa KU1241*	*D. f. rufoolivacens MSF261*	*D. f. meruloides TRDFU11*	*D. longicauda*	3708	82	91	-0.052023121	0.687385609	0.075682587	0.491839764
48	*branch J (D. f. meruloides TRDFU11)*	*D. f. rufoolivacens MSF261*	*D. tyrannina FM429946*	*D. longicauda*	4034	31	32	NA	NA	NA	NA
49	*branch J (D. f. meruloides TRDFU11)*	*D. f. rufoolivacens MSF261*	*D. m. castanoptera PPS167*	*D. longicauda*	4935	44	47	NA	NA	NA	NA
50	*branch J (D. f. meruloides TRDFU11)*	*D. f. rufoolivacens MSF261*	*D. m. badia FCR038*	*D. longicauda*	3972	39	43	NA	NA	NA	NA
51	*branch J (D. f. meruloides TRDFU11)*	*D. f. rufoolivacens MSF261*	*D. m. obidensis CN541*	*D. longicauda*	4314	35	39	NA	NA	NA	NA
52	*branch J (D. f. meruloides TRDFU11)*	*D. f. rufoolivacens MSF261*	*D. m. olivacens MPDS0810*	*D. longicauda*	3432	26	28	NA	NA	NA	NA
53	*branch J (D. f. meruloides TRDFU11)*	*D. f. rufoolivacens MSF261*	*D. m. bartletti FM391084*	*D. longicauda*	4442	37	40	NA	NA	NA	NA
54	*branch J (D. f. meruloides TRDFU11)*	*D. f. rufoolivacens MSF261*	*D. h. homochroa KU2192*	*D. longicauda*	4119	42	43	NA	NA	NA	NA
55	*branch J (D. f. meruloides TRDFU11)*	*D. f. rufoolivacens MSF261*	*D. h. ruficeps MJM8576*	*D. longicauda*	4677	49	54	-0.048543689	0.494284564	0.098210005	0.621105225
56	*branch J (D. f. meruloides TRDFU11)*	*D. f. rufoolivacens MSF261*	*D. h. acedesta MJM9219*	*D. longicauda*	4659	48	57	-0.085714286	0.879512369	0.097456601	0.379123529
57	*branch J (D. f. meruloides TRDFU11)*	*D. f. rufoolivacens MSF261*	*D. turdina KU3783*	*D. longicauda*	2359	23	29	NA	NA	NA	NA
58	*branch J (D. f. meruloides TRDFU11)*	*D. f. rufoolivacens MSF261*	*D. t. taunayi FM399181*	*D. longicauda*	4795	59	62	-0.024793388	0.271514961	0.091314999	0.785994994
59	*branch J (D. f. meruloides TRDFU11)*	*D. f. rufoolivacens MSF261*	*D. f. atrirostris PPS293*	*D. longicauda*	4984	88	98	-0.053763441	0.73307909	0.073339209	0.463510193
60	*branch J (D. f. meruloides TRDFU11)*	*D. f. rufoolivacens MSF261*	*D. a. typhia KU536*	*D. longicauda*	3684	63	113	-0.284090909	3.930414122	0.072280147	8.48E-05
61	*branch L (D. f. meruloides TRDFU11)*	*D. a. typhia KU536*	*D. tyrannina FM429946*	*D. longicauda*	3790	49	35	NA	NA	NA	NA
62	*branch L (D. f. meruloides TRDFU11)*	*D. a. typhia KU536*	*D. m. castanoptera PPS167*	*D. longicauda*	4570	52	56	-0.037037037	0.383552679	0.096563104	0.701310019
63	*branch L (D. f. meruloides TRDFU11)*	*D. a. typhia KU536*	*D. m. badia FCR038*	*D. longicauda*	3511	35	49	NA	NA	NA	NA
64	*branch L (D. f. meruloides TRDFU11)*	*D. a. typhia KU536*	*D. m. obidensis CN541*	*D. longicauda*	3815	34	40	NA	NA	NA	NA

65	*branch L (D. f. meruloides TRDFU11)*	*D. a. typhia KU536*	*D. m. olivacens MPDS0810*	*D. longicauda*	3243	35	40	NA	NA	NA	NA
66	*branch L (D. f. meruloides TRDFU11)*	*D. a. typhia KU536*	*D. m. bartletti FM391084*	*D. longicauda*	4169	41	51	-0.108695652	1.042654834	0.104248931	0.297108183
67	*branch L (D. f. meruloides TRDFU11)*	*D. a. typhia KU536*	*D. h. homochroa KU2192*	*D. longicauda*	3934	64	56	0.066666667	0.729103292	0.091436518	0.465938481
68	*branch L (D. f. meruloides TRDFU11)*	*D. a. typhia KU536*	*D. h. ruficeps MJM8576*	*D. longicauda*	4251	63	61	0.016129032	0.176855937	0.091198704	0.85962155
69	*branch L (D. f. meruloides TRDFU11)*	*D. a. typhia KU536*	*D. h. acedesta MJM9219*	*D. longicauda*	4290	64	67	-0.022900763	0.259892478	0.088116299	0.794946714
70	*branch L (D. f. meruloides TRDFU11)*	*D. a. typhia KU536*	*D. turdina KU3783*	*D. longicauda*	2284	38	34	NA	NA	NA	NA
71	*branch L (D. f. meruloides TRDFU11)*	*D. a. typhia KU536*	*D. t. taunayi FM399181*	*D. longicauda*	4377	54	77	-0.175572519	2.054134013	0.085472768	0.039962723
72	*branch L (D. f. meruloides TRDFU11)*	*D. a. typhia KU536*	*D. f. atrirostris PPS293*	*D. longicauda*	4572	80	117	-0.187817259	2.630321784	0.07140467	0.008530408
73	*branch M (D. f. meruloides TRDFU11)*	*D. f. atrirostris PPS293*	*D. tyrannina FM429946*	*D. longicauda*	4920	68	48	0.172413793	1.871607423	0.092120704	0.061260936
74	*branch M (D. f. meruloides TRDFU11)*	*D. f. atrirostris PPS293*	*D. m. castanoptera PPS167*	*D. longicauda*	6174	92	80	0.069767442	0.918774606	0.075935318	0.358213477
75	*branch M (D. f. meruloides TRDFU11)*	*D. f. atrirostris PPS293*	*D. m. badia FCR038*	*D. longicauda*	4656	78	65	0.090909091	1.078526862	0.084290057	0.280798701
76	*branch M (D. f. meruloides TRDFU11)*	*D. f. atrirostris PPS293*	*D. m. obidensis CN541*	*D. longicauda*	4989	80	65	0.103448276	1.244347425	0.08313456	0.213371724
77	*branch M (D. f. meruloides TRDFU11)*	*D. f. atrirostris PPS293*	*D. m. olivacens MPDS0810*	*D. longicauda*	4141	55	49	0.057692308	0.586211868	0.098415455	0.557733147
78	*branch M (D. f. meruloides TRDFU11)*	*D. f. atrirostris PPS293*	*D. m. bartletti FM391084*	*D. longicauda*	5541	80	56	0.176470588	2.088913015	0.084479625	0.036715554
79	*branch M (D. f. meruloides TRDFU11)*	*D. f. atrirostris PPS293*	*D. h. homochroa KU2192*	*D. longicauda*	5108	90	83	0.040462428	0.527674995	0.076680586	0.597724931
80	*branch M (D. f. meruloides TRDFU11)*	*D. f. atrirostris PPS293*	*D. h. ruficeps MJM8576*	*D. longicauda*	5840	101	94	0.035897436	0.501390639	0.071595744	0.616096227
81	*branch M (D. f. meruloides TRDFU11)*	*D. f. atrirostris PPS293*	*D. h. acedesta MJM9219*	*D. longicauda*	5838	95	99	-0.020618557	0.288089175	0.07157005	0.773278479
82	*branch M (D. f. meruloides TRDFU11)*	*D. f. atrirostris PPS293*	*D. turdina KU3783*	*D. longicauda*	2773	89	54	0.244755245	3.002774056	0.081509711	0.00267531
83	*branch M (D. f. meruloides TRDFU11)*	*D. f. atrirostris PPS293*	*D. t. taunayi FM399181*	*D. longicauda*	5904	206	111	0.299684543	5.611497458	0.053405449	2.01E-08
84	*branch N (D. f. meruloides TRDFU11)*	*D turdina KU3783*	*D. tyrannina FM429946*	*D. longicauda*	2474	35	30	NA	NA	NA	NA
85	*branch N (D. f. meruloides TRDFU11)*	*D turdina KU3783*	*D. m. castanoptera PPS167*	*D. longicauda*	2778	45	44	NA	NA	NA	NA
86	*branch N (D. f. meruloides TRDFU11)*	*D turdina KU3783*	*D. m. badia FCR038*	*D. longicauda*	2222	38	38	NA	NA	NA	NA
87	*branch N (D. f. meruloides TRDFU11)*	*D turdina KU3783*	*D. m. obidensis CN541*	*D. longicauda*	2404	27	43	NA	NA	NA	NA
88	*branch N (D. f. meruloides TRDFU11)*	*D turdina KU3783*	*D. m. olivacens MPDS0810*	*D. longicauda*	2114	30	35	NA	NA	NA	NA
89	*branch N (D. f. meruloides TRDFU11)*	*D turdina KU3783*	*D. m. bartletti FM391084*	*D. longicauda*	2628	44	45	NA	NA	NA	NA
90	*branch N (D. f. meruloides TRDFU11)*	*D turdina KU3783*	*D. h. homochroa KU2192*	*D. longicauda*	2515	42	50	-0.086956522	0.830129234	0.104750584	0.40646572
91	*branch N (D. f. meruloides TRDFU11)*	*D turdina KU3783*	*D. h. ruficeps MJM8576*	*D. longicauda*	2623	45	62	-0.158878505	1.656532258	0.095910299	0.097614078
92	*branch N (D. f. meruloides TRDFU11)*	*D turdina KU3783*	*D. h. acedesta MJM9219*	*D. longicauda*	2636	44	62	-0.169811321	1.752691683	0.09688602	0.079654944
93	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. tyrannina FM429946*	*D. longicauda*	2798	14	8	NA	NA	NA	NA
94	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. m. castanoptera PPS167*	*D. longicauda*	3129	11	9	NA	NA	NA	NA
95	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. m. badia FCR038*	*D. longicauda*	2300	12	9	NA	NA	NA	NA
96	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. m. obidensis CN541*	*D. longicauda*	2541	11	9	NA	NA	NA	NA
97	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. m. olivacens MPDS0810*	*D. longicauda*	2337	11	8	NA	NA	NA	NA
98	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. m. bartletti FM391084*	*D. longicauda*	2955	10	10	NA	NA	NA	NA

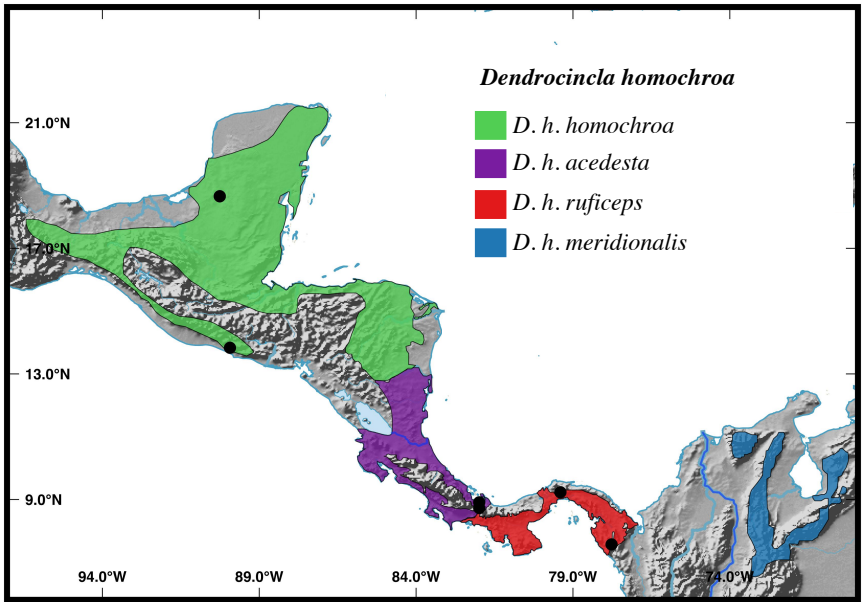
99	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. h. homochroa KU2192*	*D. longicauda*	2803	12	10	NA	NA	NA	NA
100	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. h. ruficeps MJM8576*	*D. longicauda*	2791	13	9	NA	NA	NA	NA
101	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. h. acedesta MJM9219*	*D. longicauda*	2858	13	8	NA	NA	NA	NA
102	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. f. atrirostris PPS293*	*D. longicauda*	3124	23	15	NA	NA	NA	NA
103	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. a. typhia KU536*	*D. longicauda*	2568	14	16	NA	NA	NA	NA
104	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. f. fuliginosa KU1241*	*D. longicauda*	2534	11	11	NA	NA	NA	NA
105	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. f. rufoolivacens MSF261*	*D. longicauda*	2544	14	11	NA	NA	NA	NA
106	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. f. ridgwayi JK04254*	*D. longicauda*	2679	16	16	NA	NA	NA	NA
107	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. f. neglecta CUJ160*	*D. longicauda*	2147	14	9	NA	NA	NA	NA
108	*D turdina KU3783*	*D. t. taunayi FM399181*	*D. f. meruloides TRDFU11*	*D. longicauda*	2621	12	12	NA	NA	NA	NA
109	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. tyrannina FM429946*	*D. longicauda*	4354	12	7	NA	NA	NA	NA
110	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. m. castanoptera PPS167*	*D. longicauda*	5363	14	15	NA	NA	NA	NA
111	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. m. badia FCR038*	*D. longicauda*	3948	13	11	NA	NA	NA	NA
112	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. m. obidensis CN541*	*D. longicauda*	4210	7	13	NA	NA	NA	NA
113	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. m. olivacens MPDS0810*	*D. longicauda*	3608	10	7	NA	NA	NA	NA
114	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. m. bartletti FM391084*	*D. longicauda*	4857	14	12	NA	NA	NA	NA
115	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. turdina KU3783*	*D. longicauda*	2575	8	7	NA	NA	NA	NA
116	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. t. taunayi FM399181*	*D. longicauda*	5047	15	11	NA	NA	NA	NA
117	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. f. atrirostris PPS293*	*D. longicauda*	5479	11	13	NA	NA	NA	NA
118	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. a. typhia KU536*	*D. longicauda*	4109	14	12	NA	NA	NA	NA
119	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. f. fuliginosa KU1241*	*D. longicauda*	3962	12	11	NA	NA	NA	NA
120	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. f. rufoolivacens MSF261*	*D. longicauda*	4206	14	11	NA	NA	NA	NA
121	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. f. ridgwayi JK04254*	*D. longicauda*	4785	16	11	NA	NA	NA	NA
122	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. f. neglecta CUJ160*	*D. longicauda*	3560	12	9	NA	NA	NA	NA
123	*branch F (D. h. homochroa KU2192)*	*D. h. ruficeps MJM8576*	*D. f. meruloides TRDFU11*	*D. longicauda*	4575	11	9	NA	NA	NA	NA
124	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. tyrannina FM429946*	*D. longicauda*	4427	15	8	NA	NA	NA	NA
125	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. m. castanoptera PPS167*	*D. longicauda*	5411	13	17	NA	NA	NA	NA
126	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. m. badia FCR038*	*D. longicauda*	4001	12	13	NA	NA	NA	NA
127	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. m. obidensis CN541*	*D. longicauda*	4227	8	11	NA	NA	NA	NA
128	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. m. olivacens MPDS0810*	*D. longicauda*	3610	10	5	NA	NA	NA	NA
129	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. m. bartletti FM391084*	*D. longicauda*	4928	13	13	NA	NA	NA	NA
130	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. h. ruficeps MJM8576*	*D. longicauda*	4627	65	45	0.181818182	1.924619752	0.094469664	0.054276946
131	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. turdina KU3783*	*D. longicauda*	2625	7	7	NA	NA	NA	NA
132	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. t. taunayi FM399181*	*D. longicauda*	5103	16	10	NA	NA	NA	NA

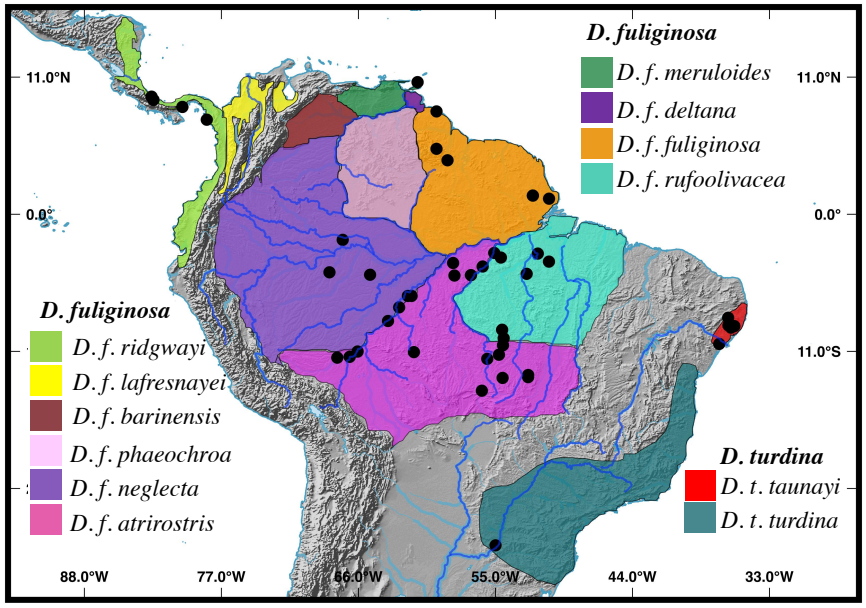
133	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. f. atrirostris PPS293*	*D. longicauda*	5538	16	13	NA	NA	NA	NA
134	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. a. typhia KU536*	*D. longicauda*	4165	13	13	NA	NA	NA	NA
135	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. f. fuliginosa KU1241*	*D. longicauda*	4036	12	11	NA	NA	NA	NA
136	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. f. rufoolivacens MSF261*	*D. longicauda*	4204	14	14	NA	NA	NA	NA
137	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. f. ridgwayi JK04254*	*D. longicauda*	4857	16	10	NA	NA	NA	NA
138	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. f. neglecta CUJ160*	*D. longicauda*	3619	10	4	NA	NA	NA	NA
139	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. f. meruloides TRDFU11*	*D. longicauda*	4577	11	8	NA	NA	NA	NA
140	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. tyrannina FM429946*	*D. longicauda*	3884	12	13	NA	NA	NA	NA
141	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. m. obidensis CN541*	*D. longicauda*	4016	24	28	NA	NA	NA	NA
142	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. m. olivacens MPDS0810*	*D. longicauda*	3138	34	49	NA	NA	NA	NA
143	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. m. bartletti FM391084*	*D. longicauda*	4173	51	63	-0.105263158	1.130050213	0.093149098	0.258455067
144	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. h. homochroa KU2192*	*D. longicauda*	4118	10	17	NA	NA	NA	NA
145	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. h. ruficeps MJM8576*	*D. longicauda*	4664	15	19	NA	NA	NA	NA
146	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. h. acedesta MJM9219*	*D. longicauda*	4725	14	19	NA	NA	NA	NA
147	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. turdina KU3783*	*D. longicauda*	2346	11	6	NA	NA	NA	NA
148	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. t. taunayi FM399181*	*D. longicauda*	4715	12	14	NA	NA	NA	NA
149	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. f. atrirostris PPS293*	*D. longicauda*	5041	17	17	NA	NA	NA	NA
150	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. a. typhia KU536*	*D. longicauda*	3751	13	14	NA	NA	NA	NA
151	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. f. fuliginosa KU1241*	*D. longicauda*	3669	14	14	NA	NA	NA	NA
152	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. f. rufoolivacens MSF261*	*D. longicauda*	4140	16	13	NA	NA	NA	NA
153	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. f. ridgwayi JK04254*	*D. longicauda*	4600	24	14	NA	NA	NA	NA
154	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. f. neglecta CUJ160*	*D. longicauda*	3668	16	17	NA	NA	NA	NA
155	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. f. meruloides TRDFU11*	*D. longicauda*	4398	19	14	NA	NA	NA	NA
156	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. tyrannina FM429946*	*D. longicauda*	4008	16	14	NA	NA	NA	NA
157	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. m. obidensis CN541*	*D. longicauda*	3669	20	22	NA	NA	NA	NA
158	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. m. bartletti FM391084*	*D. longicauda*	4038	49	70	-0.176470588	1.936412773	0.091132733	0.052817166
159	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. h. homochroa KU2192*	*D. longicauda*	4004	15	18	NA	NA	NA	NA
160	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. h. ruficeps MJM8576*	*D. longicauda*	4216	15	15	NA	NA	NA	NA
161	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. h. acedesta MJM9219*	*D. longicauda*	4215	17	18	NA	NA	NA	NA
162	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. turdina KU3783*	*D. longicauda*	2379	6	10	NA	NA	NA	NA
163	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. t. taunayi FM399181*	*D. longicauda*	4548	15	18	NA	NA	NA	NA
164	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. f. atrirostris PPS293*	*D. longicauda*	4828	15	18	NA	NA	NA	NA
165	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. a. typhia KU536*	*D. longicauda*	3668	14	19	NA	NA	NA	NA
166	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. f. fuliginosa KU1241*	*D. longicauda*	3675	14	16	NA	NA	NA	NA

167	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. f. rufoolivacens MSF261*	*D. longicauda*	3727	15	10	NA	NA	NA	NA
168	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. f. ridgwayi JK04254*	*D. longicauda*	3999	19	15	NA	NA	NA	NA
169	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. f. neglecta CUJ160*	*D. longicauda*	3049	12	10	NA	NA	NA	NA
170	*branch A (D. m. castanoptera PPS167)*	*D. m. olivacens MPDS0810*	*D. f. meruloides TRDFU11*	*D. longicauda*	3944	15	12	NA	NA	NA	NA
171	*branch C (D. m. castanoptera PPS167)*	*D. m. obidensis CN541*	*D. tyrannina FM429946*	*D. longicauda*	4590	47	38	NA	NA	NA	NA
172	*branch C (D. m. castanoptera PPS167)*	*D. m. obidensis CN541*	*D. h. homochroa KU2192*	*D. longicauda*	4643	41	46	NA	NA	NA	NA
173	*branch C (D. m. castanoptera PPS167)*	*D. m. obidensis CN541*	*D. h. ruficeps MJM8576*	*D. longicauda*	5087	48	48	NA	NA	NA	NA
174	*branch C (D. m. castanoptera PPS167)*	*D. m. obidensis CN541*	*D. h. acedesta MJM9219*	*D. longicauda*	5082	53	49	0.039215686	0.396460317	0.098914531	0.691765477
175	*branch C (D. m. castanoptera PPS167)*	*D. m. obidensis CN541*	*D. turdina KU3783*	*D. longicauda*	2680	25	29	NA	NA	NA	NA
176	*branch C (D. m. castanoptera PPS167)*	*D. m. obidensis CN541*	*D. t. taunayi FM399181*	*D. longicauda*	5364	53	53	0	0	0.097426476	1
177	*branch C (D. m. castanoptera PPS167)*	*D. m. obidensis CN541*	*D. f. atrirostris PPS293*	*D. longicauda*	5633	56	59	-0.026086957	0.279580365	0.093307541	0.779799473
178	*branch C (D. m. castanoptera PPS167)*	*D. m. obidensis CN541*	*D. a. typhia KU536*	*D. longicauda*	4218	41	48	NA	NA	NA	NA
179	*branch C (D. m. castanoptera PPS167)*	*D. m. obidensis CN541*	*D. f. fuliginosa KU1241*	*D. longicauda*	4277	36	43	NA	NA	NA	NA
180	*branch C (D. m. castanoptera PPS167)*	*D. m. obidensis CN541*	*D. f. rufoolivacens MSF261*	*D. longicauda*	4669	41	44	NA	NA	NA	NA
181	*branch C (D. m. castanoptera PPS167)*	*D. m. obidensis CN541*	*D. f. ridgwayi JK04254*	*D. longicauda*	4928	49	46	NA	NA	NA	NA
182	*branch C (D. m. castanoptera PPS167)*	*D. m. obidensis CN541*	*D. f. neglecta CUJ160*	*D. longicauda*	3899	40	42	NA	NA	NA	NA
183	*branch C (D. m. castanoptera PPS167)*	*D. m. obidensis CN541*	*D. f. meruloides TRDFU11*	*D. longicauda*	4846	47	46	NA	NA	NA	NA
184	*branch D (D. m. obidensis CN541)*	*D. tyrannina FM429946*	*D. h. homochroa KU2192*	*D. longicauda*	4019	96	85	0.060773481	0.815450353	0.074527506	0.414814572
185	*branch D (D. m. obidensis CN541)*	*D. tyrannina FM429946*	*D. h. ruficeps MJM8576*	*D. longicauda*	4211	95	90	0.027027027	0.368793433	0.073285001	0.7122817
186	*branch D (D. m. obidensis CN541)*	*D. tyrannina FM429946*	*D. h. acedesta MJM9219*	*D. longicauda*	4240	102	93	0.046153846	0.641278206	0.071971643	0.521341947
187	*branch D (D. m. obidensis CN541)*	*D. tyrannina FM429946*	*D. turdina KU3783*	*D. longicauda*	2442	47	58	-0.104761905	1.069274896	0.097974716	0.284945819
188	*branch D (D. m. obidensis CN541)*	*D. tyrannina FM429946*	*D. t. taunayi FM399181*	*D. longicauda*	4555	83	121	-0.18627451	2.680372403	0.069495757	0.00735403
189	*branch D (D. m. obidensis CN541)*	*D. tyrannina FM429946*	*D. f. atrirostris PPS293*	*D. longicauda*	4717	83	133	-0.231481481	3.531813058	0.065541827	0.000412721
190	*branch D (D. m. obidensis CN541)*	*D. tyrannina FM429946*	*D. a. typhia KU536*	*D. longicauda*	3646	72	109	-0.20441989	2.805829806	0.072855413	0.005018719
191	*branch D (D. m. obidensis CN541)*	*D. tyrannina FM429946*	*D. f. fuliginosa KU1241*	*D. longicauda*	3714	57	99	-0.269230769	3.483129703	0.077295649	0.000495588
192	*branch D (D. m. obidensis CN541)*	*D. tyrannina FM429946*	*D. f. rufoolivacens MSF261*	*D. longicauda*	4000	63	107	-0.258823529	3.496074622	0.07403261	0.000472157
193	*branch D (D. m. obidensis CN541)*	*D. tyrannina FM429946*	*D. f. ridgwayi JK04254*	*D. longicauda*	4120	71	115	-0.23655914	3.303814396	0.071601825	0.00095379
194	*branch D (D. m. obidensis CN541)*	*D. tyrannina FM429946*	*D. f. neglecta CUJ160*	*D. longicauda*	3308	54	94	-0.27027027	3.433097373	0.078724907	0.000596728
195	*branch D (D. m. obidensis CN541)*	*D. tyrannina FM429946*	*D. f. meruloides TRDFU11*	*D. longicauda*	4067	65	121	-0.301075269	4.311962924	0.069823251	1.62E-05
196	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. tyrannina FM429946*	*D. longicauda*	5286	25	26	NA	NA	NA	NA
197	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. m. obidensis CN541*	*D. longicauda*	4782	38	34	NA	NA	NA	NA
198	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. h. homochroa KU2192*	*D. longicauda*	5448	28	30	NA	NA	NA	NA
199	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. h. ruficeps MJM8576*	*D. longicauda*	5721	34	30	NA	NA	NA	NA
200	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. h. acedesta MJM9219*	*D. longicauda*	5765	34	28	NA	NA	NA	NA

201	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. turdina KU3783*	*D. longicauda*	3029	17	14	NA	NA	NA	NA
202	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. t. taunayi FM399181*	*D. longicauda*	6097	31	22	NA	NA	NA	NA
203	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. f. atrirostris PPS293*	*D. longicauda*	6594	39	30	NA	NA	NA	NA
204	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. a. typhia KU536*	*D. longicauda*	4842	26	27	NA	NA	NA	NA
205	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. f. fuliginosa KU1241*	*D. longicauda*	4896	25	29	NA	NA	NA	NA
206	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. f. rufoolivacens MSF261*	*D. longicauda*	4862	26	23	NA	NA	NA	NA
207	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. f. ridgwayi JK04254*	*D. longicauda*	5442	30	26	NA	NA	NA	NA
208	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. f. neglecta CUJ160*	*D. longicauda*	3978	19	22	NA	NA	NA	NA
209	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. f. meruloides TRDFU11*	*D. longicauda*	5232	22	27	NA	NA	NA	NA
210	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. tyrannina FM429946*	*D. longicauda*	3360	23	25	NA	NA	NA	NA
211	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. m. bartletti FM391084*	*D. longicauda*	3546	58	50	0.074074074	0.761664427	0.0972529	0.446260312
212	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. m. olivacens MPDS0810*	*D. longicauda*	2741	43	32	NA	NA	NA	NA
213	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. m. castanoptera PPS167*	*D. longicauda*	3836	63	47	0.145454545	1.544084762	0.09420114	0.1225678
214	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. m. badia FCR038*	*D. longicauda*	3089	47	46	NA	NA	NA	NA
215	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. h. homochroa KU2192*	*D. longicauda*	3450	32	27	NA	NA	NA	NA
216	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. h. ruficeps MJM8576*	*D. longicauda*	3713	28	30	NA	NA	NA	NA
217	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. h. acedesta MJM9219*	*D. longicauda*	3765	32	29	NA	NA	NA	NA
218	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. turdina KU3783*	*D. longicauda*	2063	13	16	NA	NA	NA	NA
219	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. t. taunayi FM399181*	*D. longicauda*	3823	25	26	NA	NA	NA	NA
220	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. f. atrirostris PPS293*	*D. longicauda*	4089	37	28	NA	NA	NA	NA
221	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. f. fuliginosa KU1241*	*D. longicauda*	3069	22	18	NA	NA	NA	NA
222	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. f. rufoolivacens MSF261*	*D. longicauda*	3386	27	21	NA	NA	NA	NA
223	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. f. neglecta CUJ160*	*D. longicauda*	2975	26	26	NA	NA	NA	NA
224	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. f. meruloides TRDFU11*	*D. longicauda*	3529	23	23	NA	NA	NA	NA
225	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. f. ridgwayi JK04254*	*D. longicauda*	3637	28	25	NA	NA	NA	NA
226	*D. m. obidensis CN541*	*D. m. merula KU1307*	*D. a. typhia KU536*	*D. longicauda*	3160	25	22	NA	NA	NA	NA
227	*D. m. castanoptera PPS167*	*D. m. badia FCR038*	*D. m. merula KU1307*	*D. longicauda*	3569	18	22	NA	NA	NA	NA
228	*D. m. castanoptera PPS167*	*D. m. olivacens MPDS0810*	*D. m. merula KU1307*	*D. longicauda*	3274	18	29	NA	NA	NA	NA
229	*D. m. castanoptera PPS167*	*D. m. bartletti FM391084*	*D. m. merula KU1307*	*D. longicauda*	4408	43	43	NA	NA	NA	NA
230	*D. h. homochroa KU2192*	*D. h. ruficeps MJM8576*	*D. m. merula KU1307*	*D. longicauda*	3960	10	16	NA	NA	NA	NA
231	*D. h. homochroa KU2192*	*D. h. acedesta MJM9219*	*D. m. merula KU1307*	*D. longicauda*	4053	13	16	NA	NA	NA	NA
232	*D. t. taunayi FM399181*	*D turdina KU3783*	*D. m. merula KU1307*	*D. longicauda*	2418	11	13	NA	NA	NA	NA
233	*D. f. meruloides TRDFU11*	*D. f. atrirostris PPS293*	*D. m. merula KU1307*	*D. longicauda*	4445	71	57	0.109375	1.23503166	0.088560483	0.216818721
234	*D. f. meruloides TRDFU11*	*D. a. typhia KU536*	*D. m. merula KU1307*	*D. longicauda*	3448	36	42	NA	NA	NA	NA

235	*D. f. meruloides TRDFU11*	*D. f. fuliginosa KU1241*	*D. m. merula KU1307*	*D. longicauda*	3304	32	34	NA	NA	NA	NA
236	*D. f. meruloides TRDFU11*	*D. f. rufoolivacens MSF261*	*D. m. merula KU1307*	*D. longicauda*	3604	34	36	NA	NA	NA	NA
237	*D. f. rufoolivacens MSF261*	*D. f. fuliginosa KU1241*	*D. m. merula KU1307*	*D. longicauda*	3143	25	23	NA	NA	NA	NA
238	*D. f. meruloides TRDFU11*	*D. f. ridgwayi JK04254*	*D. m. merula KU1307*	*D. longicauda*	3946	25	31	NA	NA	NA	NA
239	*D. f. meruloides TRDFU11*	*D. f. neglecta CUJ160*	*D. m. merula KU1307*	*D. longicauda*	3088	18	22	NA	NA	NA	NA


Dendrocincla homochroa
D. h. homochroa
D. h. acedesta
D. h. ruficeps
D. h. meridionalis
21.0°N
17.0°N
13.0°N
9.0°N
94.0°W
89.0°W
84.0°W
79.0°W
74.0°W


D. fuliginosa
D. f. meruloides
D. f. deltana
D. f. fuliginosa
D. f. rufoolivacea
D. fuliginosa
D. f. ridgwayi
D. f. lafresnayei
D. f. barinensis
D. f. phaeochroa
D. f. neglecta
D. f. atrirostris
D. turdina
D. t. taunayi
D. t. turdina
11.0°N
0.0°
11.0°S
88.0°W
77.0°W
66.0°W
55.0°W
44.0°W
33.0°W

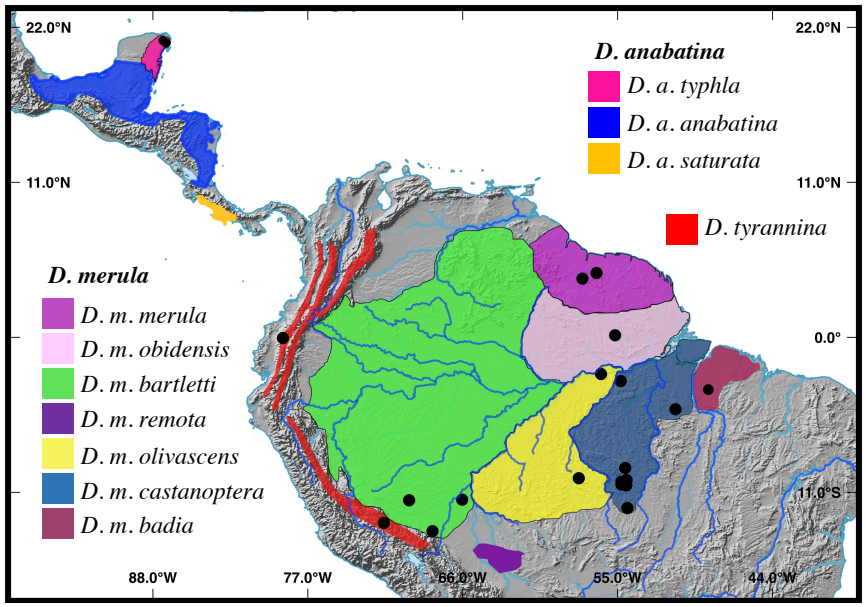

D. anabatina
D. a. typhla
D. a. anabatina
D. a. saturata
D. tyrannina
D. merula
D. m. merula
D. m. obidensis
D. m. bartletti
D. m. remota
D. m. olivascens
D. m. castanoptera
D. m. badia
22.0°N
11.0°N
0.0°
11.0°S
88.0°W
77.0°W
66.0°W
55.0°W
44.0°W

Figure 1.

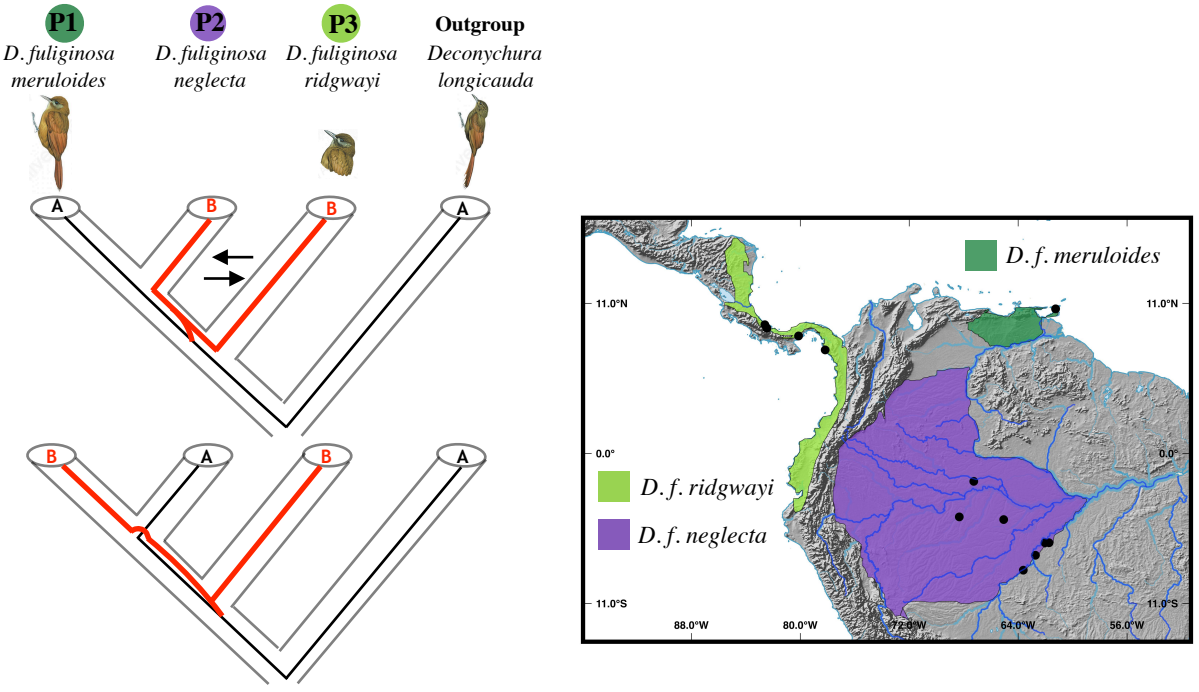

P1
D. fuliginosa meruloides
P2
D. fuliginosa neglecta
P3
D. fuliginosa ridgwayi
Outgroup
Deconychura longicauda
A
B
B
A
B
A
B
A
D. f. meruloides
D. f. ridgwayi
D. f. neglecta
11.0°N
0.0°
11.0°S
88.0°W
80.0°W
64.0°W
56.0°W

Figure 2.

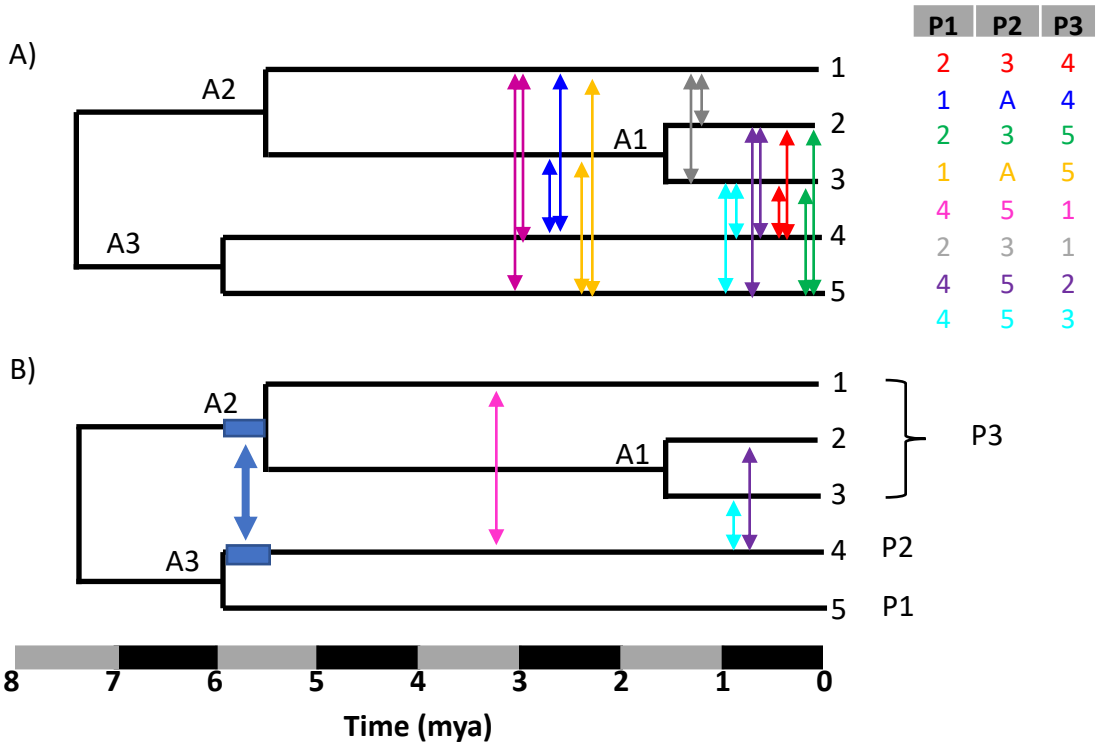

A)
A2
A1
A3
1
2
3
4
5
P1 P2 P3
2 3 4
1 A 4
2 3 5
1 A 5
4 5 1
2 3 1
4 5 2
4 5 3
B)
A2
A1
A3
1
2
3
4
5
P3
P2
P1
8 7 6 5 4 3 2 1 0
Time (mya)

Figure 3.

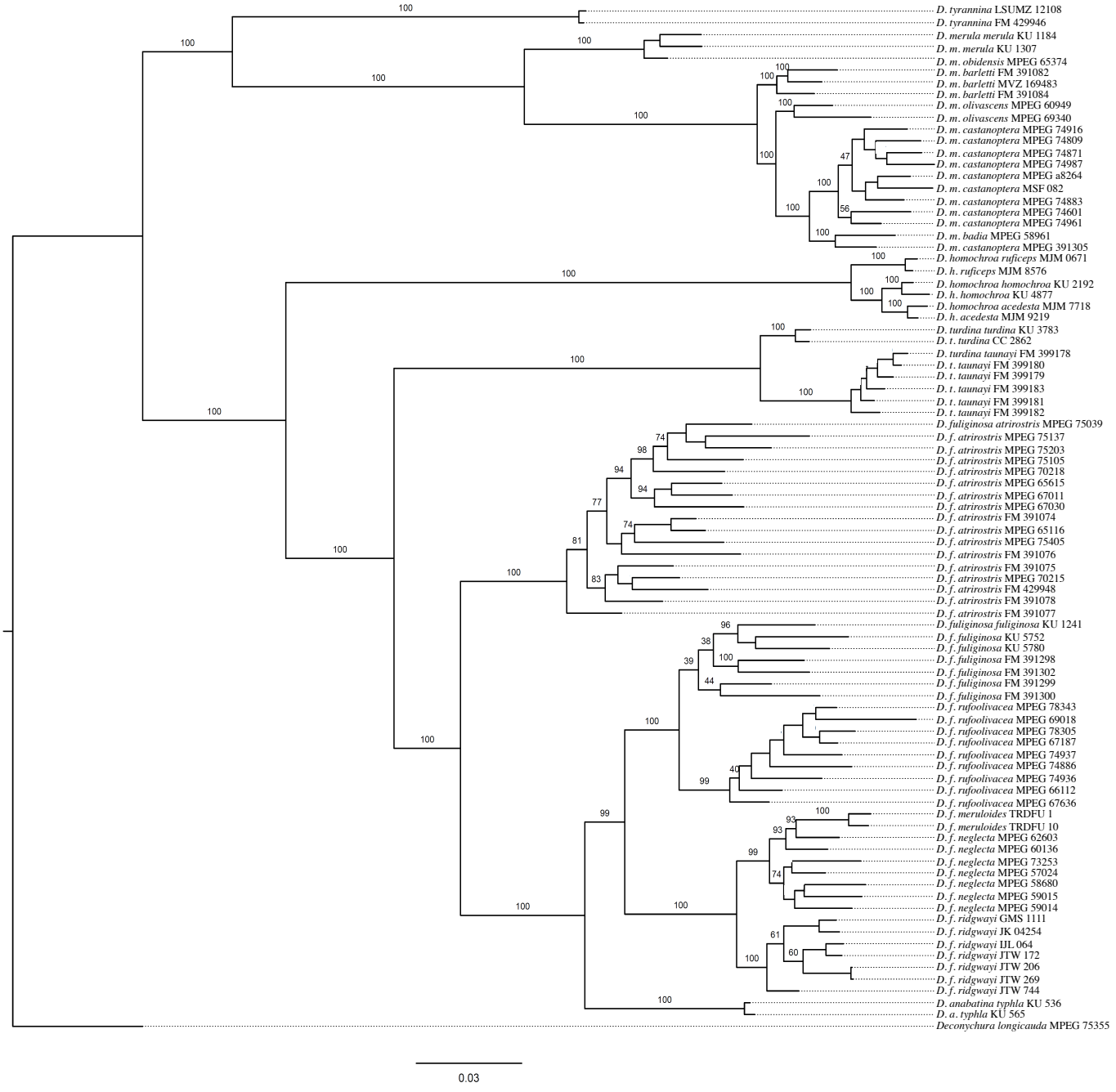

D. tyrannina LSUMZ 12108
D. tyrannina FM 429946
D. merula merula KU 1184
D. m. merula KU 1307
D. m. obidensis MPEG 65374
D. m. barletti FM 391082
D. m. barletti MVZ 169483
D. m. barletti FM 391084
D. m. olivascens MPEG 60949
D. m. olivascens MPEG 69340
D. m. castanoptera MPEG 74916
D. m. castanoptera MPEG 74809
D. m. castanoptera MPEG 74871
D. m. castanoptera MPEG 74987
D. m. castanoptera MPEG a8264
D. m. castanoptera MSF 082
D. m. castanoptera MPEG 74883
D. m. castanoptera MPEG 74601
D. m. castanoptera MPEG 74961
D. m. badia MPEG 58961
D. m. castanoptera MPEG 391305
D. homochroa ruficeps MJM 0671
D. h. ruficeps MJM 8576
D. homochroa homochroa KU 2192
D. h. homochroa KU 4877
D. homochroa acedesta MJM 7718
D. h. acedesta MJM 9219
D. turdina turdina KU 3783
D. t. turdina CC 2862
D. turdina taunayi FM 399178
D. t. taunayi FM 399180
D. t. taunayi FM 399179
D. t. taunayi FM 399183
D. t. taunayi FM 399181
D. t. taunayi FM 399182
D. fuliginosa atrirostris MPEG 75039
D. f. atrirostris MPEG 75137
D. f. atrirostris MPEG 75203
D. f. atrirostris MPEG 75105
D. f. atrirostris MPEG 70218
D. f. atrirostris MPEG 65615
D. f. atrirostris MPEG 67011
D. f. atrirostris MPEG 67030
D. f. atrirostris FM 391074
D. f. atrirostris MPEG 65116
D. f. atrirostris MPEG 75405
D. f. atrirostris FM 391076
D. f. atrirostris FM 391075
D. f. atrirostris MPEG 70215
D. f. atrirostris FM 429948
D. f. atrirostris FM 391078
D. f. atrirostris FM 391077
D. fuliginosa fuliginosa KU 1241
D. f. fuliginosa KU 5752
D. f. fuliginosa KU 5780
D. f. fuliginosa FM 391298
D. f. fuliginosa FM 391302
D. f. fuliginosa FM 391299
D. f. fuliginosa FM 391300
D. f. rufoolivacea MPEG 78343
D. f. rufoolivacea MPEG 69018
D. f. rufoolivacea MPEG 78305
D. f. rufoolivacea MPEG 67187
D. f. rufoolivacea MPEG 74937
D. f. rufoolivacea MPEG 74886
D. f. rufoolivacea MPEG 74936
D. f. rufoolivacea MPEG 66112
D. f. rufoolivacea MPEG 67636
D. f. meruloides TRDFU 1
D. f. meruloides TRDFU 10
D. f. neglecta MPEG 62603
D. f. neglecta MPEG 60136
D. f. neglecta MPEG 73253
D. f. neglecta MPEG 57024
D. f. neglecta MPEG 58680
D. f. neglecta MPEG 59015
D. f. neglecta MPEG 59014
D. f. ridgwayi GMS 1111
D. f. ridgwayi JK 04254
D. f. ridgwayi IJL 064
D. f. ridgwayi JTW 172
D. f. ridgwayi JTW 206
D. f. ridgwayi JTW 269
D. f. ridgwayi JTW 744
D. anabatina typhla KU 536
D. a. typhla KU 565
Deconychura longicauda MPEG 75355
0.03

Figure 4.

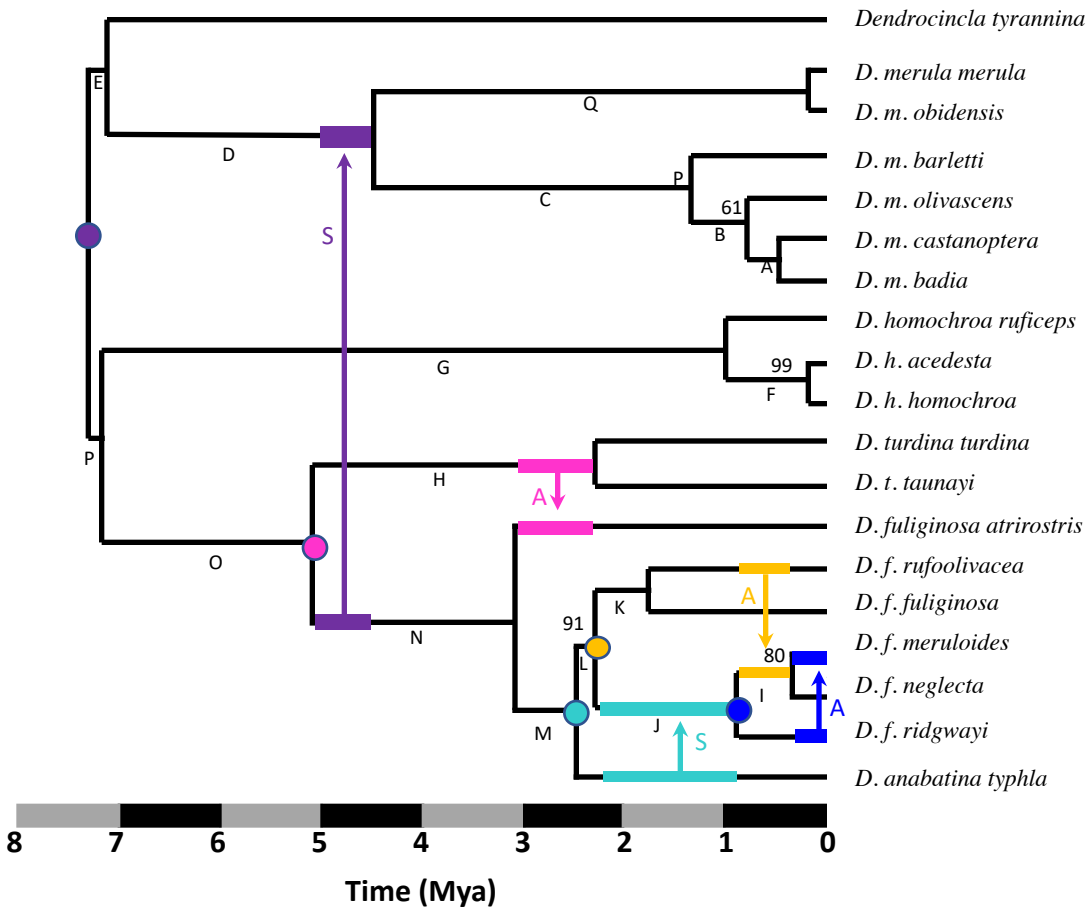
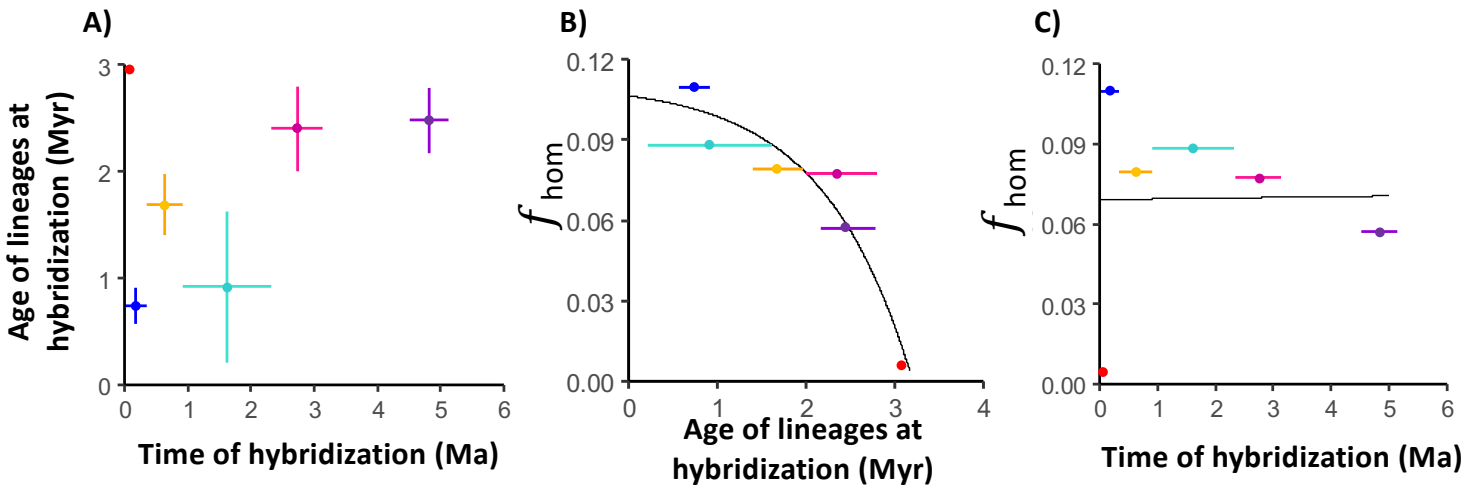

Dendrocincla tyrannina
D. merula merula
D. m. obidensis
D. m. barletti
D. m. olivascens
D. m. castanoptera
D. m. badia
D. homochroa ruficeps
D. h. acedesta
D. h. homochroa
D. turdina turdina
D. t. taunayi
D. fuliginosa atrirostris
D. f. rufoolivacea
D. f. fuliginosa
D. f. meruloides
D. f. neglecta
D. f. ridgwayi
D. anabatina typhla
E
D
Q
C
P
61
B
A
S
G
99
F
P
H
A
O
N
K
91
L
A
80
I
A
M
J
S
8
7
6
5
4
3
2
1
0
Time (Mya)

Figure 5.

Figure 6.


A)
Age of lineages at hybridization (Myr)
Time of hybridization (Ma)
B)
f_{hom}
Age of lineages at hybridization (Myr)
C)
f_{hom}
Time of hybridization (Ma)